SYSTEMATIC REVIEW OF FOSSIL AND RECENT *CREPIDULA* AND DISCUSSION OF EVOLUTION OF THE CALYPTRAEIDAE

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ABSTRACT

The genus *Crepidula* is 1 branch of an adaptive radiation by a group of mesogastropods into ecological space formerly monopolized by bivalves. I present the systematics of Recent and fossil species, based on study of qualitative and quantitative shell characters and, if possible, radula and life history data. Coexamination of fossil and living material increases the reliability of evolutionary inferences. I define the key characters for species identification and understanding of evolutionary history of the group. I correlate behavioral and life history traits with morphology, a step which aids understanding of form, function, and evolution.

I propose changes in taxonomy, including alterations in the disposition of known synonyms, and synonymization of 17 species. *C. uncata* is possibly a subspecies of *C. adunca; C. praerupta* and its synonym *C. ungana* are possibly variants of *C. princeps.* I also formally resurrect *C. marginalis, C. cymbaeformis,* and *C. nivea.* I suggest the strong possibility that *C. plana* equals *C. unguiformis,* and that *C. lessonii* equals *C. striolata,* but these cannot be decided without anatomical comparisons.

I point out species affinities and ecological associations, and present zoogeographic data over time. Evolutionary history of the family is given. I establish the following major points:

The best species-level taxonomic characters are the shape of the septal margin, beak conformation and whorl expansion rate (correlated characters), sculpture, color patterns, type of larval development, and muscle scars. The last 2 have been inconsistently used by *Crepidula* workers. Ecological and morphological traits are often correlated, such as the size of the septum and brooding habits. Maximum adult size, degree of convexity, and obliqueness of the shell are valuable characters, but variable due to environmental influences.

Genetic morphological variation (e.g., polymorphism) at the intraspecific level is low, compensated by environmentally-mediated phenotypic plasticity. This enhances the evolutionary conservatism of the genus. Capacity for plasticity is itself a trait, showing interspecific variation. Several species (*C. fornicata, C. aculeata*) were more variable in the Miocene than today.

Division of *Crepidula* into subgenera or sections is not warranted, except possibly for *Siphopatella. Ianacus* is polyphyletic.

There are 5 basic ecological-morphological groupings within *Crepidula.* Rarely are more than 1 species from each group found sympatrically. Sympatric species differ in life history strategies. There is high species diversity in the tropics; in cold temperate climates, species intermediate in size are absent, and there is a broadening of the niches and a higher density of individuals per species in those extreme forms remaining.

In general, large species have numerous planktonic larvae, often form stacks, and occur in dense colonies. Small species are lecithotrophic, and do not stack. Species with planktonic larvae are hardly more widely distributed than nonplanktonic ones, but are superior colonizers over short time periods.

Species distribution patterns over geologic time suggest that the center of evolution of the Calyptraeidae was the Panamic region of the late Cretaceous and early Tertiary. There have been no major range contractions, but several warm-water species of *Crepidula* have shifted due to changes in climate. I speculate on causes of extinction for *C. princeps,* the largest *Crepidula* known.

The European region is impoverished in Calyptraeidae, whereas the Australia-New Zealand region is a center of speciation for *Crepidula.*

Speciation is favored in organisms which brood their young and are specialized in choice of substrate; it is enhanced in regions with disrupted habitats. However, in species such as *C. adunca,* isolation is broken by considerable inter-deme communication and, presumably, selection. One might predict species change without speciation, as discussed by Wright (1955).

Modes of evolution probably differ between species with pelagic and brooded young because of differences in the size of the adult population, numbers of offspring, and degree of communication among populations.

Most *Crepidula* species are generalists with respect to temperature and salinity; this has allowed them to be stable species in unstable environments. Those species with narrow geographic ranges are physiological specialists.

I present a scheme for the evolution of the family Calyptraeidae. The main element is the fate of the septum (columella). The sequence of development of traits in the family was dependent on adaptation of the gill for filter-feeding, followed (in indeterminable order) by remodeling of the body for sedentary life, evolution of protandry, and acquisition of the ability to retain the developing young under the foot.

I compare *Crucibulum* with *Crepidula* regarding shell morphology, ecology, distribution, and abundance, and point out the parallel evolution of life styles. I also compare *Trichotropis,* and conclude that it is convergent in lifestyle, not a direct ancestor to *Crepidula.*

There are inherent difficulties in constructing a phylogenetic tree for any group of organisms. I present what is known of evolutionary affinities within the genus *Crepidula.* I give possible examples of parallel and convergent evolution, including the white, planar *Crepidula* species which have radiated into a habitat new for the mesogastropods: sedentary life inside dead shells. Another radiation is that of *Crepidula* species into the intertidal zone. (Most species are primarily subtidal.) The stacking habit and brooding are traits which are likely to have converged in several *Crepidula* lineages.

The ecological role of the Calyptraeidae converges on that of oysters, not gastropod limpets. Similarities include filter-feeding, sedentary life, partially brooded larval development, and cases of sequential hermaphroditism.

INTRODUCTION

Crepidula Lamarck (Gastropoda: Calyptraeidae) is a genus of marine mesogastropods well represented in modern shallow-water faunas. There are at least 40 valid species worldwide, of which ¼ are known only as fossils. The fossil history of the genus stems from scant records in the late Cretaceous (Buvignier, 1852; Seeley, 1861; Stoliczka, 1867; Wilckens, 1922; Shimer & Shrock, 1959). At least 1 representative of the family, *Calyptraea pileolus,* dates from the Lower Cretaceous (von Ihering, 1907), if stratigraphic records are correct. The richest fossil deposits are along the coasts of North America and in Argentina, with some representation in the Mediterranean region and Japan. Today, species of *Crepidula* dominate many marine communities in both biomass and in the role of energy cycling, when compared with other filter feeders present.

This paper presents a review and revision of the systematics of the genus in the Northern Atlantic and Eastern Pacific, with special attention to fossil forms. I have treated some forms from other parts of the world when information was available and when inclusion of such information clarified understanding of the evolution and ecology of the genus. It is necessary to determine the valid species before attempting to analyze species variation and distribution patterns in time, and to understand the relative ecological positions of the several species. Systematics of the fossil forms is necessarily based on shell characters. Systematic revision of Recent species has been taken as far as shell characters allow so that it could be fitted with the fossil data. However, many decisions must await examination of living material. This paper is consequently not a complete, formal monograph of the group, but in it I attempt to establish sound criteria for judging species characters and assessing traits important in understanding evolution of the Calyptraeidae.

After presentation of the species and their distinguishing characters, I outline the evolutionary history of *Crepidula* and its place within the Calyptraeidae. I show that the family occupies an ecological position close to that of the epifaunal bivalves, and that *Crepidula* has evolved phenotypic plasticity to accommodate environmental change. Possible examples of parallel and convergent evolution are illustrated at the species and generic levels, respectively. Zoogeographic data are outlined to show patterns of expansion and contraction of species ranges, possibly related to world climate and other factors. The degree of genetic control of morphology, along with correlations among morphological and behavioral characters, are related to the hierarchy of characters I used in systematic analyses, and to the living habits of members of this ecologically unique and taxonomically puzzling group of gastropods.

METHODS

A. *Material examined*

Fossil and Recent *Crepidula* species were examined from systematic and stratigraphic collections at major museums.[1] Locality, morphometric data, type of matrix, and qualitative shell characters were recorded for each lot, as well as relative abundances for all calyptraeids. Data on distribution of species were also obtained from the literature, but because of misidentifications, errors in synonymy, and poor stratigraphic dating, such data often are unreliable. Hence information obtained in this way was used only if supported by illustrations and if the dating could be made to conform with current geological thinking (Jenks, 1956; Congrès Géologique International, 1955-1967; Hazel, 1971; Akers, 1972).

Tertiary material from the Atlantic Coastal Plain, collected by R. Thomas in 1967-1969 and C. Jones in 1969-1971 and deposited at the MCZ, Harvard University, was used for in-depth study of assemblages. Field notes of these collectors were valuable in determining conditions of deposition, preservation, and the degree to which the assemblages were natural and in-place.

This work does not include some species restricted to Africa and the Indian Ocean. These species are represented in American museums almost exclusively by beach-worn shells; original descriptions and illustrations are unclear for several. I have not located the type-specimen of *C. porcellana,* which is key to the group. The African species not treated are listed in Table 1A. Also listed in Table 1A are the named fossil species from Japan (from Taki, 1938). Since Japanese workers tend to split, there are probably fewer valid species than indicated. Table 1B lists problematic species and *nomina nuda.* A complete worldwide monograph of the genus should include anatomical characters in order to resolve the problems created by similar shell morphologies.

B. *Measurements and statistical analysis*

TABLE 1A. African and fossil Japanese species beyond the scope of this work.

Species	Author	Year	Locality
(1) Africa			
adspersa	Dunker	1846[1]	Benguela
goreensis	(Gmelin)	1791	Senegal; Indian Ocean
lentiginosa	Sowerby	1883[2]	S. Africa
porcellana	(Linnaeus)	1758	Senegal; Indian Ocean
sulin	Dautzenberg (ex Adanson)	1912	S. Africa; Indian Ocean
(2) Japan fossils[3]			
auricula	Yokoyama	1924	
convexa	Yokoyama	1925	
isimotoi	Otuka	1934	
jimboana	Yokoyama	1931	
navia	Yokoyama	1925	
nidatoriensis	Otuka	1934	
turugasakana	Nomura & Hatai	1935	

[1]Types in Berlin Museum.
[2]Possible types in British Museum (Nat. Hist.).
[3]Full references are in Taki (1938: 145-146).

Measurements for taxonomic study were taken, using calipers, as illustrated in Fig. 1. An ocular micrometer fitted on a binocular microscope was used for additional measurements on the 4 smallest species. The measurements include total length (L), greatest width (W), height perpendicular to the aperture (H), beak length (B), septum length (S) and septal area (Sa), length of the anterior portion of the aperture, excluding the septum (A), and area of the same anterior portion (Aa), distance from anterior to posterior (measured by a string) following the curvature of the shell along the median dorsal line (D), and obliqueness of the shell (O). The areas of the septum (Sa) and anterior aperture (Aa) were obtained by tracing the perimeters of septum and aperture, and measuring the distance with a planimeter. Obliqueness was calculated as the difference between the angles of the right and left sides of the shell, found by drawing lines perpendicular to the base of the shell and lines intersecting at the highest point of the shell, as seen from the posterior view (Fig. 1B). Convexity was calculated as D/L; it therefore cannot take values between 1 and 0. As a

TABLE 1B. Nomina dubia and nuda, including species wrongly named in other genera, for which no other information is presently available.

Genus	Species	Author	Year	Locality	Comments
Crepidula	*altavillensis*	Defrance	1818	France	Fossil. Type in Caen or Geneva.
Crepidula	*atra*	Philippi	1851	None	Type lost.
Crepidula	*calyptraeiformis*	Deshayes	1830	Peru	Fossil. Type perhaps at Ecole des Mines, Paris.
Calyptraea	*chiliensis*	Lesson	1832	Chile	Recent. Type in Paris Museum.
Crepidula	*coriocella*	Philippi	1887	Chile	Fossil. Type in Santiago, Chile, if extant. Not a calyptraeid.
Calyptraea	*crepidularis*	Lamarck	1802	Grignon	Fossil.
Calyptraea	*depressa*	Lesson	1832	Chile	Recent. Type in Paris Museum.
Crepidula	*holurthii*	"Parrey"	?	None	Sowerby, 1883: 74.
Crepidula	*mytilina*	Philippi	1887	Chile	Fossil (= *C. unguiformis?*).
Calyptraea	*navicella*	Lesson	1832	Peru	Recent.
Crypta	*navicula*	Dunker, n.n.; Mörch	1877	None	Recent. Type lost.
Crepidula	*paranensis*	Borchert	1901	Argentina	Miocene.
Crepidula	*parisiensis*	Deshayes	1830	Grignon	Fossil (= *Calyptraea crepidularis*).
Crepidula	*pedum*	Mörch	1877	None	
Crepidula	*pileoides*	Schlotheim	1832	None	Nomen nudum.
Crepidula	*rugosa*	Anton	1839	None	Fossil.
Crepidula	*solea*	Blainville	1818	None	Recent.
Crepidula	*squamosa*	Menke	1828	Brazil	Recent.
Crypta	*striata*	Hutton	1873	New Zealand	Fossil.
Crepidula	*subspirata*	Blainville	1824	None	Nomen nudum.

convention, the "convexities" of concave shells, in which D is greater than L, but the shell bends inwards, were assigned negative values. The length-to-width ratio (L/W) also was calculated.

There is confusion in the literature as to the orientation of *Crepidula* shells. The antero-posterior axis is shown in Fig. 1. All references to left and right are to the animal's own left and right, i.e. viewed from the posterior dorsal aspect of the shell.

Values obtained for discrimination of degree of convexity ranged from concave (negative values), planar (1.00 to 1.15), low convex (1.15 to 1.25), and moderately convex (1.25 to 1.35), to highly convex (over 1.35). Obliqueness varied from equi-angular (0°) to highly oblique (30°). In all reported measurements, the sample size, mean, and coefficient of variation are given (in text and Table 2). In order to reduce bias of substrate upon shell shape, individuals from 4 or more localities representing different substrates were measured for each species, when possible. Fossil and living representatives of the same species were analyzed separately, then compared.

The major problem with quantified data in the systematics of *Crepidula* is the lack of a discernible adult stage as recorded in the shell. Growth continues throughout the lifetime of an individual, although there is some reduction in growth rate after sexual maturity. Measurements of living snails show that obliqueness seems not to change in a regular way with growth. As for convexity, there is some tendency for an increase with age, but some individuals flatten out as they grow, and many remain constant in shape. Variability within age classes is large.

It is possible in some populations of a few species to tell if and when the change from male to female (final maturity) occurred because there is rapid shell growth with a change in slope at the time of sex change (see illustrations in Coe, 1942b). In other populations, crowding of growth lines at a given point in growth indicates maturity. However, these clues cannot be relied on in all cases to separate adult females from the rest of the population. For this reason, rigorous statistical tests between species cannot be applied to the means and coefficients of variation of the convexity index, which may be related to the age composition of the samples.

Still, computation of convexity and obliqueness from the largest of available shells gives some assurance that adults are being used. Collectors tend to over-repre-
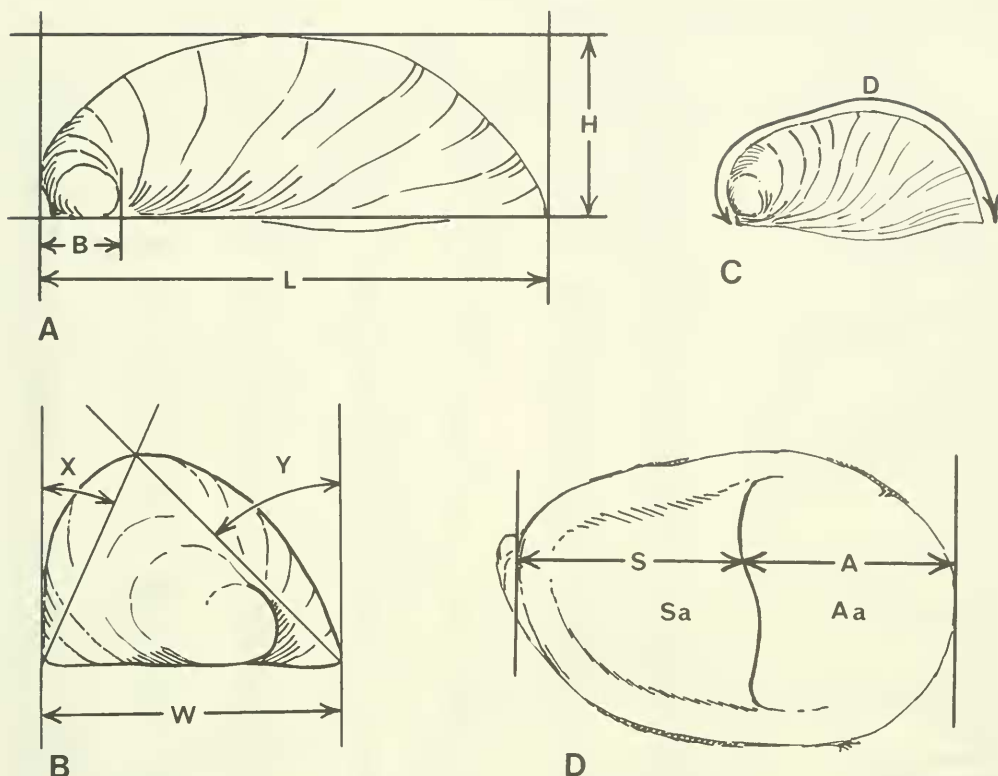
FIG. 1. Measurements taken to determine inter- and intraspecific variability of shell characters. The illustrated specimens are *Crepidula fornicata*. A. Right lateral view; B = beak length; H = height; L = length. B. Posterior view; W = width; X and Y measure the angles determining degree of asymmetry (obliqueness) of the shell; obliqueness = Y − X. C. Right lateral view; D = length of dorsal arch. D. Ventral view; A = length of anterior portion of the aperture excluding that covered by the septum; Aa = area of aperture excluding that covered by the septum; S = length of septum; Sa = area of septum.

sent adult animals in their samples. Number of whorls at adulthood varies with the species but can also be used to indicate maturity in shells which are not eroded at the apex. Real differences in convexity and obliqueness do exist between species; these are complex factors mentally integrated in the shell identification process by anyone familiar with *Crepidula*. The quantitative methods used here are an attempt to delineate them.

Size characteristics at the species level are difficult to determine. As there is no sure way of measuring adults only, the sample is distorted by juvenile snails. To estimate maximum length of the species, the largest individual was measured. Means and standard deviations of the lengths among mixed age classes are meaningless for taxonomic evaluation.

C. *Definition of key characters*

Due to the immense morphological variability and intergradation present in the Calyptraeidae, it has been a difficult group for taxonomists. Some workers have considered nearly every form a different species (Broderip, 1835; Conrad, 1844) while others (Tryon, 1886; Dall, 1892) synonymized the majority under a few names. There are, however, several clear-cut characters which are species-specific in *Crepidula*. They follow, and are given functional and evolutionary significance in Table 3.

1. *Muscle scars.* A muscle scar is present at, or absent from, the right-hand corner of the septum where it joins the shell, or forward of it. Depth and shape of the scar (lunar, ovate, etc.) are also indicative of the species but can vary according to shell width and thickness (Fig. 2). Only a few fossil shells are so worn that this character is obliterated. Some "aging" of the shell

TABLE 2. Summary of quantitative taxonomic data.

Species	Convexity (mm)		Obliqueness (°)		L/W (no units)		L. max. (mm)[2]
	Mean	C.V.[1]	Mean	C.V.	Mean	C.V.	
aculeata	1.29	10.07	16	48	1.31	9.16	32.0
aculeata spinosa (variant)	1.95	6.67	33	26	1.42	9.15	55.0
adunca Recent	1.66	8.43	8	44	1.45	13.79	21.0
adunca fossil Pacific							28.0
adunca fossil Atlantic	1.62		11		1.37		25.0
convexa Recent	1.43	10.49	12	30	1.43	12.59	18.5
convexa Miocene							24.0
costata	1.34	11.19	9	50	1.53	3.27	43.0
cymbaeformis	1.34	7.46	20	20	1.68	5.36	41.5
dilatata	1.52	9.21	10	23	1.19	8.40	59.0
diminutiva							17.0
dorsata	1.24	11.19	12	16	1.02	12.75	26.0
excavata	1.36	13.97	34	35	1.56	8.33	52.0
fornicata Recent	1.54	17.53	18	54	1.42	11.97	59.0
fornicata Miocene	1.73	16.18	34	55	1.55	14.84	65.0
gibbosa	1.20	13.33	12	19	1.29	55.81	32.0
grandis	1.54	5.19	16	11	1.35	5.19	57.0
immersa	1.05	1.90	2	127	1.53	9.15	42.5
incurva	1.34	8.96	5	83	1.47	8.16	25.0
lessonii	1.07	2.80	0.3	167	1.79	32.40	28.0
striolata (variant?)							35.0
lirata	1.70	8.24	32	17	1.86	11.83	50.0
maculosa Recent	1.44	11.81	10	36	1.36	5.88	37.5
maculosa Miocene	1.26	15.08	9	28	1.39	8.63	38.0
marginalis	1.18	8.04	4	26	1.20	15.10	32.0
monoxyla	1.04	6.73	0	0	1.50	8.67	33.0
monoxyla contorta (variant)	1.42	7.75	0	0	1.78	5.62	
naticarum	1.50	4.00	13	70	1.73	3.47	31.0
nivea							45.0
norrisiarum	1.31	9.92	6	75	1.40	3.57	35.0
nummaria	1.10	7.27	1	177	1.38	15.22	40.0
onyx	1.41	12.06	12	30	1.55	10.32	67.0
perforans	−1.05	6.75	0.3	21	1.79	63.62	35.0
pileum					1.30	5.38	15.5
princeps					1.50	7.33	125.0
protea	1.19	4.10	5	11	1.30	16.92	33.0
unguiformis	−1.08	0.93	3	283	1.43	24.47	38.0
plana W. Atlantic	1.00	11.00	0	0	1.66	10.24	
cochleare (variant)	1.20	55.83	4	66	1.44	4.86	
walshi	−1.08	6.48	5	89	0.79	13.92	26.0

[1]Coefficient of variation.
[2]To nearest 0.5 mm.

after death often makes the scar more visible. A muscle scar above the left side of the septum is occasionally present.

In at least some species lacking a muscle scar (e.g., *Crepidula fornicata, C. plana*), a small secondary shell muscle extends from the visceral sac to the roof of the shell. Additionally, there is a U-shaped muscle, varying in degree of development, from the posterior rim of the foot to the rear rim of the septum (illustrated in Kleinsteuber, 1913). Neither leaves permanent etching on the shell. There is another muscle attachment along the anterior edge of the septum in some species (e.g., *C. fornicata*) representing remnants of the columellar muscle; neither of the 2 above-mentioned muscles appear to be derived from the columellar muscle.

The usual place of insertion of the muscle attaching body to shell in coiled mesogastropods is on the columella (via the columellar muscle). The septum of *Crepidula* is homologous to the columella. Migration of the point of the muscle insertion to the junction of the septum and shell proper, or onto the shell, is a specialization for sedentary limpet-like existence, as is the derivation of new muscles for shell attachment. The presence of an insertion on either side of the septum as shown by the presence of 2 muscle scars is a 3rd solution to the problem of attachment of body to shell and substrate.
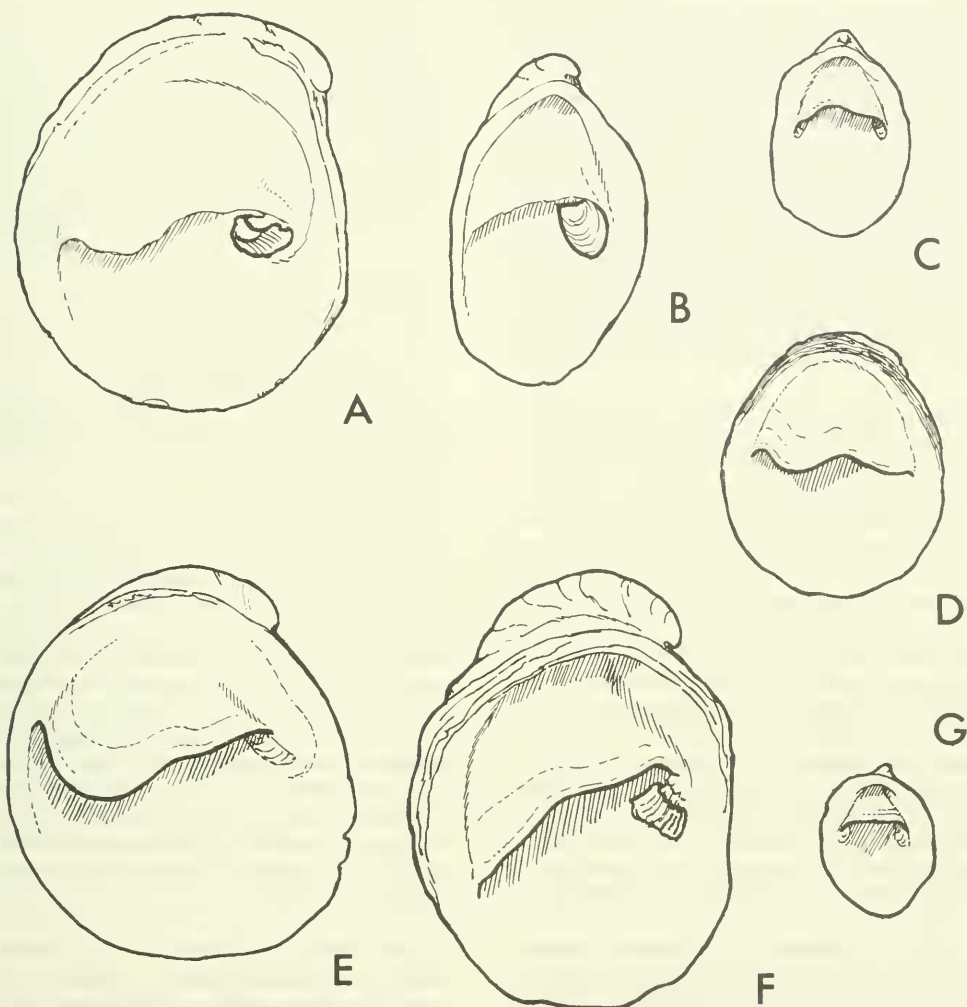
FIG. 2. Diagnostic features of the *Crepidula* shell. A. Lunar-shaped muscle scar; sinuate (notched) septal margin. (*C. aculeata* var. *spinosa*.) B. Beak excavated; chevron-shaped muscle scar; straight septal margin extending farther forward on the left side. (*C. excavata*.) C. Beak excavated; 2 small ovate muscle scars; septum laterally extended. (*C. norrisiarum*.) D. No muscle scar; sinuate septal margin. (*C. nummaria*.) E. Narrow muscle scar; septum with deep left sulcus. (*C. dilatata*.) F. Rectangular muscle scar; nearly straight septal margin extending farther forward on the left side. (*C. grandis*.) G. Beak excavated; 2 faint muscle scars which are tear-shaped; short septum with lateral extensions. (*C. adunca*.)

2. *Shape of the septum.* Presence or absence of a ridge along the midline of the septum, the pattern of notches and curves in its margin, and the position of its lateral attachments are species-specific, although depth of insertion and depth of notches are variable (Fig. 2). In some species, the septum can be so deeply situated that the beak of the shell is excavated; that is, it contains a cavity ventral to the septum. Convexity or concavity of the septum (from ventral view) has been used as a

species character, but in some specimens it is ambiguous. The septum is often broken or obscured in fossils.

3. *Size of the septum.* Relative area of the septum versus that of the entire aperture differs among the species, although there is some variability depending on the age of the specimen. The septum supports the viscera and provides for muscle attachment. It divides the body into 3 parts: the foot, the viscera, and the head and brood cham-

ber regions. Propodia, or flaps extending anteriorly from the foot, and neck lappets further separate the brood area from the foot and the gills, respectively.

The disk-like foot covers the area of the septum and no more; thus the larger the septum proportional to the size of the shell, the greater will be the area of the foot. Also, the deeper the septum is inserted into the shell, the thicker may be the foot. Changes in the ratio of septal to apertural area in ontogeny must be distinguished from differences between species, and must be interpreted in their own right.

4. *Beak characters*. The apical portion or beak of the shell is a particularly useful key to species diagnosis (Fig. 3). It may be rostrate (hooked and free from the shell) or appressed to the shell; it may be at the level of, or above the shell margin. It may lie nearly on the antero-posterior axis, be inclined to the right, or coiled to form a complete whorl or more. In no species is the shell perfectly bilaterally symmetric. The beak region can extend beyond the aperture posteriorly and/or laterally, or it can be invisible from ventral view. Beak characters depend on ontogenetic changes in the whorl expansion rate of the shell and upon the degree of asymmetric growth. The protoconch is worn in adult specimens, but its size in comparison with adult size is of taxonomic and ecological importance.

5. *Shell sculpture*. All species possess growth lines, and a few have costae radiating from the apex. Ribs also are produced environmentally if an individual grows on a ribbed surface, such as a scallop. Some members of ribbed species produce plicate spines along the ribs.

6. *Color pattern*. Although absent or faint in fossils, shell color patterns are significant in living species. Intensity and shading are not of taxonomic value. At least 1 case of color polymorphism exists in *Crepidula* (*C. convexa*), but it is not a major problem in species recognition.

7. *Adult size*. Maximum size is species-specific, but individuals of several species will mature at a reduced size if space is limited.
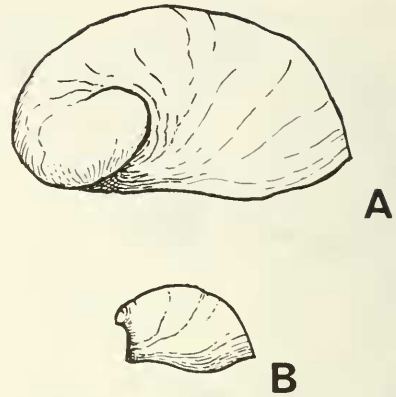
8. *Shell shape and aperture dimensions.*

FIG. 3. Possible beak configurations in *Crepidula*. A. Coiled beak (*C. aculeata* var. *spinosa*). B. Rostrate beak (*C. adunca*).

These features must be interpreted cautiously. Some species are always globose or elongate; some are invariably highly convex. Others extend over a wide range of shapes. Obliqueness of the shell is a reliable character if a mean value and range are taken. Experience with several populations of snails from diverse substrates will acquaint one with the possible shape variation to be expected for each species. Some shell characters, such as convexity and obliqueness, are positively correlated within individuals ($r = 0.67$). The correlation coefficient for convexity versus length-width ratio is only 0.14.

9. *Life history characters*. All *Crepidula* species are protandrous, copulate, and brood the young during early development. Some species produce a few (10^1-10^2) large eggs and retain the young until they develop to the crawling stage, while others produce many (10^3-10^4) small, less yolky eggs, and release planktotrophic larvae. Although some molluscan species may show a facultative ability either to release planktonic but non-feeding young, or to retain the larvae until a crawling stage is reached (Hadfield, 1972), *Crepidula* species do not.

There is no variability in type of young within or between populations of *Crepidula fornicata*, *C. convexa*, *C. plana*, *C. adunca*, or *C. onyx* (those I have studied). Egg size and yolk content are approximately constant for a given species, with dwarfed individuals (those maturing at a small size due to a restricted substrate, such as *C. convexa* on eel grass blades) simply produc-

ing fewer eggs (Conklin, 1898). Hence the type of larva seems to be genetically fixed in a particular species and is a good species character. There is variability, environmental and probably also genetic, in the length of time eggs are retained by the brooding female. It is not difficult to postulate transition from one mode of larval development to another through evolutionary time, perhaps more than once.

The planktonic larval form is associated with other life history factors and morphological traits. For example, early maturity, large intrinsic rate of natural increase (r), pelagic young, and large adult size tend to evolve as a functional unit in *Crepidula.* Therefore, the type of larva is a more valuable character than it would be if it were independent. Patterns of mortality, birth rates, and other quantitative life history characters differ among the species, but data are available for only a few. The type of larval development is used here as a taxonomic character because it is easily scored and is known for a large number of species, and symbolizes a particular reproductive pattern.

10. *Stacking.* Some species facultatively form large stacks that are permanent during the lifetime of the individuals using each other as a substrate. Others form only temporary mating clusters of 2 or 3 individuals. Some fossils buried in place reveal the stacking habit, although absence of preserved stacks does not prove that a given fossil species could not form them. Species capable of stacking are found to be very concentrated in fossil beds—often such areas have been called *Crepidula* beds by paleontologists (Dall, 1910).

11. *Anatomy.* Details of internal anatomy are, of course, impossible to obtain for the fossils, and comparative anatomical work on this genus has thus far been superficial (Heath, 1916; Moritz, 1938, 1939; Ishiki, 1939; Coe, 1942a; Werner & Grell, 1950; Werner, 1951, 1955). The anatomical papers unfortunately do not reveal clear species-specific differences. Gray (1857) and Parodiz (1939) are among the few to give sketches of radular teeth, and to show some variation in cusp arrangement which is of taxonomic value. However, intraspecific variation is a complicating factor, and the teeth are quite similar in some species.

I discuss the radulae of those species whose bodies were available to me.

12. *Periostracum.* All species form a periostracum, although it is often worn away almost as fast as shell material is consolidated under it. Smith (1946) used this character to distinguish species. A few species have characteristically thick, shaggy periostracums while most have delicate ones. Color and the appearance of shagginess of the periostracum are influenced by algal growth. Fossil shells have no indication of this trait.

D. *Arrangement of species and species*
   variants in the following pages

Within a few species of *Crepidula* are specimens consistently different from the common type, albeit in minor features. In some cases, for instance in *C. convexa,* there are forms originally named as separate species, but which merely take their peculiar shape from a particular substrate. These I designate ecophenotypes or substrate forms, without attaching a scientific name.

However, especially with fossils, one often cannot be certain if small but consistent differences are due to the genotype or strictly to environment. Such aberrant forms, in which geographical and genetic relationship to the common form are unclear, have at times been called subspecies or even have been elevated to full species rank. But the term "subspecies" implies a degree of genetic and geographic isolation. Frequently in the malacological literature, the forms in question are called "varieties" or "variants," terms without formal taxonomic standing but assigned a scientific name, e.g. *Crepidula aculeata* var. *spinosa.* The structure of a trinomial is somewhat cumbersome, but at least the information inherent in the name is not lost. These deviant forms are of ecological importance, and further information could clarify their relationship to the stock from which they appear to be derived. In this paper, I use the term "variant" to describe forms which are either subspecies or ecophenotypes, but for which insufficient data are available to decide the question. If the variant is already known by a scientific name, I use it descriptively.

The species descriptions are arranged

alphabetically, except for species groups so designated by headings in the text. These are the *Crepidula adunca* group, the *C. unguiformis* group including *C. plana,* and the Pacific white planar *Crepidula* species, which for comparative purposes I treat as units. I give the number of specimens examined at the end of each species description. Specific lot numbers and localities of illustrated specimens are available on request.

A question mark beginning an entry in a synonymy indicates that I have not been able personally to confirm another person's judgment as to the placement of the species name in synonymy, and that I am not sure that it is correct. Similarly, a question mark beginning a listing of a species range and geologic period indicates that I have reason to doubt another worker's data.

TAXONOMY

Genus **Crepidula** Lamarck
  Crepidula Lamarck, 1799: 78.
  Crepidula Lamarck. Dall, 1909a: 82.
      Type-species by monotypy: *Patella fornicata* Linnaeus, 1758.
      Range: Late Cretaceous; Eocene to Recent. Worldwide but especially in the Americas.

Description:

Shell limpet-like, growing from a posterior apex or "beak" in a rapidly expanding, asymmetrical whorl, terminating in a wide aperture. Dorsal midline of the shell follows a right spiral (Fig. 4). Aperture occupies nearly the length of the shell. Columella modified into an internal septum extending across the posterior half of the shell. Disk-like foot ventral to the septum; visceral mass above it. Head small; gill area large, used for filter-feeding. A pair of propodia extends anteriorly from the foot and, along with neck lappets, supports the young during brooding. Shape of the shell highly variable within a species as it is modified to fit against a hard substrate.

Remarks:

Dall (1909a) gives a complete synonymy of the genus. Thiele (1929) lists subgeneric

names with authors and dates. There is no current controversy over the genus name or what species should be placed under it, except for members of the subgenus *Crepipatella* which are similar to *Crucibulum.* Some authors have broken the genus into "sections"; I discuss the biological importance of such designations after the species are set forth. The few species intermediate in shell characters between *Crepidula* and *Crucibulum* I place with *Crepidula.*

The family name Calyptraeidae has been used in all major references since Blainville (1824); for example, see Thiele (1929), Wenz (1940: 899), Abbott (1954), and Cox in the *Treatise on Invertebrate Paleontology* (1960: 87, 94, 122). Abbott (1974), however, used Crepidulidae on the basis of Fleming (1822: 494). I suggest retaining the commonly-used family name for nomenclatural stability. Also, some authors have used "Crepidulidae" to refer only to the genus *Crepidula* (e.g., Grant & Gale, 1931). A change in the family name would cause confusion particularly in the ecological literature, where a reference to "Crepidulidae" would become ambiguous.

Shimer & Shrock (1959) record *Crepidula* from the Cretaceous but without specific documentation. I have seen no Cretaceous specimens, but the illustrations of internal molds from St. Croix by Buvignier (1852) are most convincing, as are internal molds from New Zealand (Wilckens, 1922). Dating of the St. Croix locality is suspect. Material from the Eocene is not uncommon.
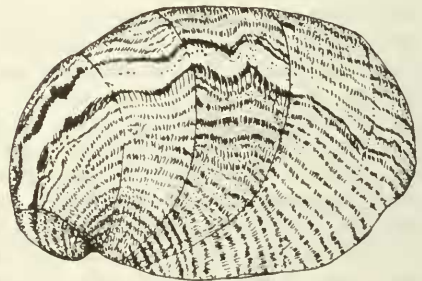

FIG. 4. Spiral growth pattern of *Crepidula fornicata,* showing the position of the median dorsal line and several growth stoppages.

KEY TO THE SPECIES TREATED

The following is a dichotomous key intended to aid in identification of the species treated in this paper, with the exception of Cretaceous and Australo-New Zealand fossils. It does not represent evolutionary pathways within the group, since features such as muscle scars and sculpture possibly are polyphyletic. Attempts to key out shell specimens of the planar *Crepidula* species will be difficult; several individuals of a population must be used. Egg capsule and geographical data help identification in some cases, but transport of specimens by man and wide natural geographic ranges make identification of species on the basis of geography risky.

1   a) Muscle scar present 2
             b) Muscle scar absent 19

2   (1)   a) Radial sculpture present 3
             b) Radial sculpture absent 8

3   (2)   a) Radial ribs with spines 4
             b) Radial ribs smooth 5

4   (3)   a) Shell thin, length less than 40 mm . . . . *C. aculeata*
             b) Shell thick, massive, length more than 40 mm . . . . *C. aculeata* var. *spinosa*

5   (3)   a) Ribs widely spaced, plicate 6
             b) Ribs fine, not plicate 7

6   (5)   a) Two muscle scars . . . . *C. costata*
             b) Single faint muscle scar . . . . *C. lirata*

7   (5)   a) Shell surface malleated . . . . *C. youngi*
             b) Shell surface non-malleated . . . .*C. incurva*

8   (2)   a) Two muscle scars 9
             b) One muscle scar 13

9   (8)   a) Shell white . . . . *C. monoxyla*
             b) Shell pigmented 10

10   (9)   a) Beak highly rostrate and far above shell margin .11
             b) Beak weakly rostrate and curved down near shell margin 12

11   (10)   a) Shell tan to dark brown, smooth . . . .*C. adunca*
             b) Shell yellow, crenulated at the margin . . . . *C. adunca* var. *uncata*

12   (10)   a) Septum covers less than ⅓ the aperture; sides not produced. Left muscle
                scar frequently not visible . . . .*C. naticarum*
             b) Septum covers more than ⅓ the aperture; sides produced, with
                white callus . . . . *C. norrisiarum*

13   (8)   a) Shell planar . . . . *C. immersa*
             b) Shell convex 14

14   (13)   a) Septal margin deeply notched at left side . . . .*C. dilatata*
             b) Septal margin not deeply notched at left side .15

15   (14)   a) Beak highly coiled laterally; shell massive 16
             b) Beak slightly inclined; adult shell not massive .17

16   (15)   a) Shell elongate (L/W 1.4 or more); fossil only . . . . *C. princeps*
             b) Shell subcircular (L/W less than 1.4) . . . .*C. grandis*

17   (15)   a) Growth highly oblique . . . . *C. excavata*
             b) Growth nearly symmetrical 18

18   (17)   a) Beak free from shell; adult shell less than 24 mm long . . . . *C. convexa*
             b) Beak appressed to shell; adults usually more than 24 mm long . . . . *C. maculosa*

19   (1)   a) Shell highly convex (D/L > 1.25) 20
             b) Shell planar or low convex 22

SPECIES DESCRIPTIONS WITH NOTES ON RANGES AND TAXONOMIC PROBLEMS

Crepidula aculeata (Gmelin)

Patella aculeata Gmelin, 1791: 3693 (middle American islands [Caribbean Sea]).

Crepidula aculeata (Gmelin). Lamarck, 1822: 25.

C. intorta (Linnaeus) var. Say, 1822: 227 (southern Coast U.S. [Atlantic]).

C. tomentosa Quoy & Gaimard, 1832-33: 419, pl. 72, figs. 1-6 (New Holland, Western Port and Jervis Bay, Cape Dromadaire) [syn. nov.].

C. maculata Quoy & Gaimard, 1832-33: 422, pl. 72, figs. 7-9 (New Zealand) [syn. nov.].

C. foliacea Broderip, 1834: 38; 1835: 202, pl. 28, fig. 9 (Arica, Peru [Chile]). Holotype: BM(NH) 1966633 [syn. nov.].

Calyptraea echinus Broderip, 1834: 39; 1835: 203, pl. 29, fig. 1 (Lobos Island, Peru).

C. hystrix Broderip, 1834: 39; 1835: 203, pl. 29, fig. 2 (Lobos Island, Peru). Syntypes: BM(NH) 1966629.

Crepidula costata Sowerby. Menke, 1847: 183 (Mazatlan). Non *C. costata* Sowerby, 1824, nec *C. costata* Morton 1829, nec *C. costata* Deshayes, 1830.

C. californica Tryon, 1886 (ex Nutt. ms., Warrington Mus.): 112, 129 (California).

C. aculeata (Gmelin). Carpenter, 1857a: 268; Brann, 1966, tablets 1321-1352.

C. gravispinosa Kuroda & Habe, 1950: 30 (Japan) [syn. nov.].

Distribution:

Atlantic

Miocene: S Florida to Maryland

Pliocene: Florida to Virginia (Waccamaw and possibly Duplin Formations) [Hazel, 1971]

Early
Pleist.: Florida (Caloosahatchee and part of Waccamaw Formations [Akers, 1972])

Pacific

Tertiary: Kanagawa, Tiba, Zyōban (Japan)

Miocene: S California (1 specimen)

Pliocene: San Diego to Los Angeles, California; Pampian deposits, Argentina (von Ihering, 1907)

Early
Pleist.: Post-Pampian deposits, Argentina; Chile N to Los Angeles

Recent: Nearly worldwide in tropics and subtropics ($34°$N-$34°$S; Keen, 1937), including Southeastern U.S., Caribbean Sea, Peru, Chile, Southern California, Hawaii, Japan, New Zealand, Southern Africa.

Description:

Shell: thin; convexity: 1.29; obliqueness: $16°$; aperture circular to ovate; L/W: 1.31 (n = 50). *Beak:* small, appressed to adult portion of shell near the margin, not excavated; does not extend far beyond the aperture. Degree of coiling variable, but at least 1 full post-larval whorl. *Septum:* very shallow, thin, concave, creased along the midline, covering less than ½ the aperture, notched on the left side and at the center of the margin. *Muscle scar:* small, lunar, deeply impressed, at the right anterior intersection of septum and shell. *Sculpture:* rows of ribs, some with plicate spines, following the spiral path of shell growth; spine development variable. *Shell color:* white with brown spots or rays, or a uniform tan. *Life history:* eggs large; no pelagic larval stage (Ishiki, 1936). Prefers rock substrate; stacks are not formed. Intertidal to offshore. *L. max.:* 32 mm. Over 200 Recent and fossil specimens, over 50 localities.

Remarks:

The numerous synonyms reflect the wide geographical range and variability of *Crepidula aculeata. C. tomentosa* was a specimen nearly devoid of spines. *C. echinus* and *C. hystrix* represent variations of spinal development in Peruvian forms. The Japanese *C. gravispinosa* is indistinguishable from *C. aculeata*; the former was named in a brief note by Kuroda & Habe with a referral to an earlier description of *C. aculeata* by Kuroda (1947, species No. 3239). Menke's *C. costata* is a Pacific variety. Say (1822) incorrectly named a specimen of *C. aculeata* as a variety of "*C. intorta*," which was really *Patella intorta* Wood (1818: 179) of England. The California shell is small, with weak spines.

Crepidula aculeata is more obviously coiled than most *Crepidula* species. It is abundant in warm waters, both in Recent times and as fossils. Considering its widespread yet disjunct distribution, and non-planktonic development, it is surprising that there are not more differences from population to population than are evidenced by shell characters.

Crepidula aculeata var. spinosa Conrad   Fig. 5

C. costata Morton, 1829: 115, pl. 7, figs. 2-3 (St. Mary's County, Maryland; Tertiary). Non *C. costata* Sowerby, 1824, nec *C. costata* Deshayes, 1830.

C. spinosa Conrad, 1843: 307 (James River, Virginia; Miocene). Syntypes: ANSP 15344.

C. ponderosa H. C. Lea, 1846: 249, pl. 35, fig. 40 (Petersburg, Virginia; Tertiary) [syn. nov.].

C. spinosa Conrad. Tuomey & Holmes, 1857: pl. 25, fig. 10.

C. costata Morton. Tuomey & Holmes, 1857: pl. 25, fig. 11.

Distribution:

Miocene: Florida to Maryland; ?Nantucket (museum labels); especially Yorktown Formation

L. Pliocene: Florida to Maryland (Choctawhatchee, Duplin Formations)

Description (points differing from the common form of *C. aculeata*):

Shell: thick, globose, highly convex (convexity: 1.95). Obliqueness: $33°$; aper-

ture ovate; L/W: 1.42 (n = 30). *Beak:* coiled and upturned, appressed to the right side of the shell above the margin; early whorl visible posteriorly and laterally from ventral view. *L. max.:* 55 mm. Over 100 specimens, 12 localities.

Remarks:

This may be a large growth form of *C. aculeata,* as first suggested by Dall (1892: 357). Its distribution is nearly contained within that of the common form of *C. aculeata* and there are indeed intergradations in size and other characters from small *C. aculeata* to massive variants in single samples from the Yorktown Miocene. The Miocene is known for its giant races of mollusks and other invertebrates. Characters which differ from those of the common form, the deeper and proportionally larger muscle scar, thicker shell, and more massive and more coiled beak, are all likely to be due to large size. There are no comparably large Recent populations of *C. aculeata.*

C. costata Sowerby (1824) is a distinct modern species from New Zealand. Therefore, if the fossil form were to be given species status, it must be named *C. spinosa,* because *C. costata* Morton (1829) is preoccupied. A subspecific rank for this fossil is not satisfactory, since we cannot distinguish between 4 possibilities: (1) all *C. aculeata* of the Miocene had the potential to grow to this large size; (2) there were genetic variants in some populations; (3) particular environmental conditions in some localities allowed this kind of growth; or (4) there existed truly allopatric populations, some of which attained this size and others of which did not.

The Miocene variants are thick as well as large. Perhaps they were able to deposit calcium carbonate more efficiently than Recent *Crepidula* species, and they greatly increased shell thickness once adulthood was reached. No massive specimens below 20 mm in length have been found. Whatever the cause of large size, it was operating on unrelated groups of organisms during the Miocene. It was therefore environmental, or such a strong selective force existed that the genomes of diverse organisms were affected in the same way.

H.C. Lea's type specimen and description for *C. ponderosa* match the massive *C. aculeata* var. *spinosa,* but some of the specimens so labeled at USNM and ANSP are actually *C. fornicata. C. spinosa* was originally named for spinous variants, but these intergrade with the non-spinous form.

Crepidula adunca Sowerby   Figs. 6-8

Eastern Pacific:

  C. adunca Sowerby, 1825: Append. p. 7 (no locality). Holotype in BM(NH).

  C. solida Hinds, 1844: 53, pl. 16, figs. 7-8 (Bodegas, California).

  C. rostriformis Gould, 1846: 160 (Straits of [Juan] de Fuca, Oregon [Washington]). Holotype: USNM 5872. Ideotypes: MCZ 169345 (Santa Barbara, California); fide Johnson (1964).

  C. uncata Menke, 1847: 184 (Panama; Mazatlan). Type lost. [Subspecies?].

  Garnotia solida (Hinds). Gray, 1857: 117.

  Crypta rostralis Conrad, 1865: 151 (Astoria, Oregon; Tertiary) [suggested by

FIG. 5. *Crepidula aculeata* var. *spinosa* from Virginia and Carolina Miocene, 4 views; a) dorsal, L = 36.1 mm; b) lateral, L = 41.0 mm; c) ventral, same specimen; d) dorsal, L = 35.8 mm; note irregular placement of spines; e) anterior, L = 41.0 mm; note plicate form of spines; f) lateral, L = 41.0 mm; note height of spines.

FIG. 6. *C. adunca* form (subspecies?) *uncata,* from Baja California, 3 views; a) dorsal, L = 15.5 mm; b) ventral, same specimen; muscle scars are accentuated with ink dots; c) lateral, same specimen; note ridges formed by growth on a ribbed shell.

FIG. 7. *C. adunca* from Monterey, California, 4 views; a) dorsal, L = 18.0 mm; b) ventral, same specimen; c) lateral, male and female pair; L of female = 18.1 mm; d) posterior, showing apex; same specimen as a and b.

FIG. 8. *C. adunca* from Virginia Miocene (originally named *C. cornucopiae*), 3 views; a) dorsal, L = 10.7 mm; b) ventral, same specimen; c) lateral, same specimen.

FIG. 9. *C. cymbaeformis* from Virginia Miocene, 3 views; a) dorsal, L = 41.5 mm; b) lateral, same specimen; c) ventral, same specimen; the shell is filled with hard matrix.
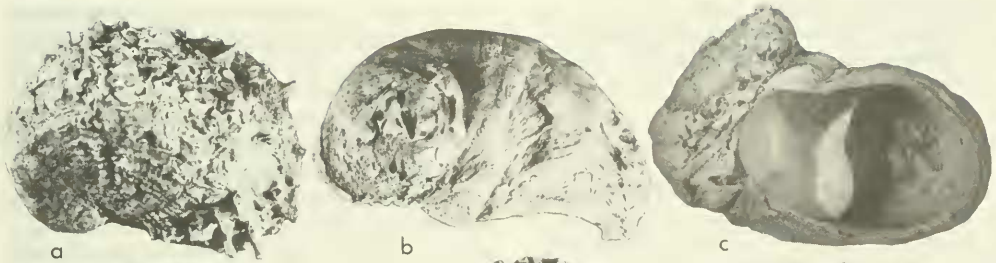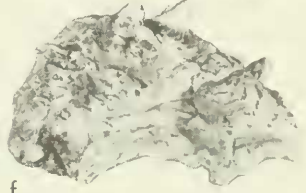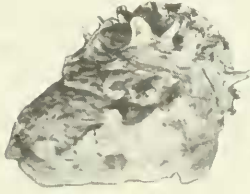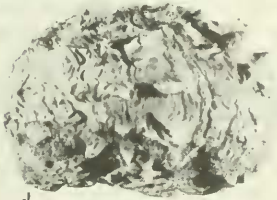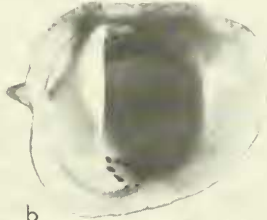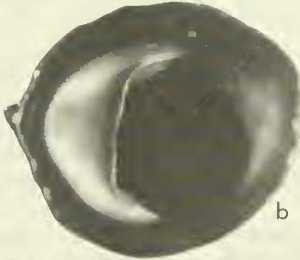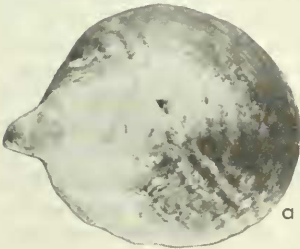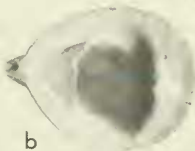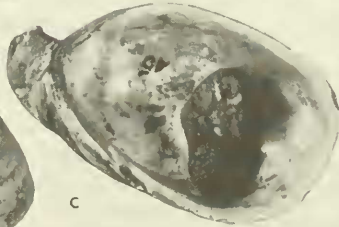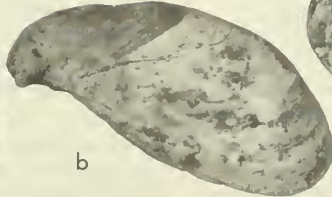
Dall, 1892: 358]. Holotype: USNM 110447.

Crepidula aeola Dall, 1927: 2 (near Cartagena, "Columbia") [= *C. uncata*].

C. adunca Sowerby. Grant & Gale, 1931: 791.

Distribution:

?Eocene: Oregon (Conrad, 1866; dating may be in error)

Miocene: San Diego to Washington (San Pablo, Astoria Formations)

Pliocene: San Diego to N California (Etchegoin, Santa Barbara Formations)

Pleist.: N Baja California to Los Angeles, California (San Pedro, Palos Verdes, and Saugus Formations)

Recent: San Diego to Vancouver Is.; a few specimens from Santo Tomas, Baja Calif. (San Felipe, Baja California, to Panama = *C. uncata*)

Western Atlantic probable synonyms:

Crepidula cornucopiae H. C. Lea 1846: 250, pl. 35, fig. 41 (Petersburg, Virginia; Tertiary).

C. rostrata Conrad, 1871: 77 (Virginia; Miocene) [syn. nov.]. Syntypes: ANSP 15323. Non *C. rostrata* C. B. Adams, 1852.

C. aesop Dall, 1903: 1610, pl. 55, figs. 6-7 (Shell Creek Pliocene, Florida) [syn. nov.]. Holotype: USNM 3300.

Distribution:

Miocene: N Carolina to Maryland (Duplin; Yorktown Formations)

Pliocene: Florida to Virginia (including later stages of Duplin and Yorktown Formations)

Early Pleist.: Florida to N Carolina (Waccamaw Formation)

?Pleist.: Nantucket (may be from Miocene material, reworked)

Description:

Shell: small, thin, cap-shaped. Convexity: 1.66 (Atlantic fossil form: 1.62); obliqueness: 8° (Atlantic fossil: 11°); L/W: 1.45 (Atlantic fossil: 1.37). Aperture subcircular (Recent, n = 50; Atlantic fossil, n = 22). *Beak:* nearly bilaterally symmetrical, rostrate, free from and well above the shell margin, hooked, usually excavated; extends behind the aperture. *Septum:* deeply inserted, planar to convex, short, covering about ¼ of the aperture; margin nearly straight, arching forward along both sides of the shell (Fig. 2G); white calluses along sides of septum. *Muscle scar:* small, tear-shaped, extending in front of the right side of the septum; a faint scar can also be visible on the left side. *Sculpture:* none except growth lines; *C. uncata* is crenulated, but from growth on *Calliostoma. Color:* outside yellow to dark brown; darker brown inside; septum white. *Life history:* no planktonic larval stage; large (0.41 mm diameter) yolky eggs (Coe, 1949). *L. max.* (Recent): 21 mm; *L. max.* (fossil—Pacific): 28 mm. *L. max.* (fossil—Atlantic): 25 mm. Recent: over 200 specimens, 38 localities. Pacific fossil: 20 specimens, 3 localities. Atlantic fossil: 30 specimens, 4 localities.

Remarks:

This species is highly variable throughout its range, but each population is rather uniform. This has led to the naming of numerous species. Because *C. adunca* has no planktonic larval stage and often inhabits small bays, living on intertidal gastropods or subtidal stones, populations do differ one from another in color and form. *C. adunca* is the ecological equivalent of *C. convexa* of the Western Atlantic.

Fossil specimens are slightly larger than Recent ones. *C. cornucopiae,* the relatively rare Western Atlantic fossil, is similar enough to be referred to *C. adunca,* although it is slightly larger. Its synonyms include *C. rostrata* Conrad and *C. aesop,* some of which have ribs caused by growth on a ribbed shell. Thus *C. adunca* or closely allied forms ranged on both sides of present-day Panama during the Miocene, but later became extinct on the Atlantic side. Shell measurements for *C. cornucopiae* and *C. adunca* are not significantly different.

The fossil named *Crypta rostralis* is a large form, and although Moore (1963) and others have considered it synonymous with *C. praerupta,* its rostrate beak and septal conformation place it with *C. adunca.* The description given of it by Addicott (1970: 65) would serve equally well for *C. adunca,* but he erroneously states that the septum of *C. adunca* covers nearly ½ the aperture and he separates it from *C. rostralis* on this basis. The type-specimen of *C.*

rostralis is definitely referable to *C. adunca*. Variable features among fossil *C. adunca* are the degree of beak coiling and the angles of the sides of the shell with the apertural plane.

C. adunca is usually dark brown, with white calluses anterior to the septum. It is most abundant at Monterey, California, but ranges widely. Some populations show color polymorphism, with tan and brown forms living together. *C. rostriformis* is an obvious synonym of *C. adunca*. The type of *C. solida* is an irregularly-shaped specimen dredged in 10 fathoms.

The Panamanian specimens named *C. rostrata* by C. B. Adams (1852: 235; paratype MCZ 186296) in some respects are intermediate between *C. adunca* and *C. incurva*. They are laterally compressed with straight septal margins and rough exteriors. The single muscle scar is very faint. Its systematic position will be resolved when more specimens are available.

The subspecies(?) named *C. uncata* from Western Mexico and Panama, usually living on *Calliostoma,* is an isolated offshoot of *C. adunca,* perhaps a good species. Its beak is very small and the shell is highly inflated; the color is yellow. These individuals possess ribs or crenulations from growth on *Calliostoma.*

Moritz (1938, 1939) has examined *C. adunca* anatomically and embryologically, and found that the veliger lacks the apical organ near the cerebral commissure found in *C. fornicata* by Conklin (1897: 111).

Crepidula aplysioides Reeve

C. aplysioides Reeve, 1859: pl. 4, fig. 19 (Rio de Janeiro).

Distribution:

Recent: Rio de Janeiro, Brasil and Argentina; possibly N to Grenada (Hog Island; Point Saline).

Description (from Reeve):

Shell: small to moderate-sized, subconvex, obliqueness about the same as in *C. fornicata*; L/W: 1.26. Aperture elliptical. *Beak:* blunt, turned to the right and appressed to the shell margin (subrostrate); not excavated. *Septum:* notched at the center, covers half the aperture; opaque white.

Muscle scar: absent. *Sculpture:* growth lines only. *Shell color:* reddish brown with obscure dark rays. *Life history:* unknown. Grenada specimens live below the tide line (0.3-16 m) and do not form stacks. *L.:* 21.5 mm (specimen illustrated in Reeve).

Remarks:

I could not find Reeve's type of *C. aplysioides* in the British Museum (Nat. Hist.).

On the island of Grenada, British West Indies, there are 1 or possibly 2 species of *Crepidula* which have been misidentified as *C. convexa* or *C. fornicata* in museum collections. They are intermediate in size between the 2, and differ in shape of the septum. Specimens taken from *Strombus gigas* opercula match the pigmentation and convexity described for *C. aplysioides,* and match the color of the opercula. Specimens from rocks, however, are darker to match the rocks and more convex, virtually identical with Reeve's illustration of *C. hepatica* Deshayes, 1830, from the Cuming collection (locality unknown). All other shell features in the 2 forms are similar. Some shells which began life liver-colored change to the lighter color. On the dark shells, dark rays are visible at the shell margin. Hence the 2 could be color morphs of 1 species, very likely that named *C. aplysioides* by Reeve. Whether the color differences represent sibling species, genetic polymorphism, or are environmentally mediated, is not known. The result is a matching of the *Crepidula* to its substrate color.

Not enough is known about the geographic range and biology of *C. aplysioides* to place it in the tables which follow. However, Parodiz (1939) illustrates the radula, though he calls it *C. onyx.*

Crepidula convexa Say

C. convexa Say, 1822: 227 (Eastern coast of the United States). Type lost.
C. glauca Say, 1822: 226 (Eastern coast of the United States). Type lost.
C. acuta H. C. Lea, 1842: 108, pl. 1, fig. 4 (Delaware Bay).
C. convexa Say. Verrill & Smith, 1874: 650, pl. 23, fig. 128.
?*C. navicula* Mörch, 1877 (ex Dunker Ms.): 105 (St. Martin; St. Thomas). Type lost.

Distribution:

Miocene: S North Carolina to Nantucket, Massachusetts (including early stages of Yorktown, Duplin Formations)

Pliocene: N Florida to Virginia (including later stages of Yorktown and Duplin Formations)

Pleist.: Waccamaw, Caloosahatchee Formations, Florida to New Jersey; Sankoty Head, Massachusetts

Recent: E Florida to Nova Scotia; West Indies at least to Puerto Rico (Abbott, 1954 and museum labels). Introduced: San Francisco, California.

Description:

Shell: small, thin; convexity: 1.43; obliqueness: $12°$; aperture ovate; L/W: 1.43. Measurements of fossils not significantly different except obliqueness: $15°$ (n = 50). *Beak:* slightly inclined to the right, free from the margin but level with it, rarely excavated, does not extend far beyond the aperture. *Septum:* deeply inserted, planar or slightly convex, ridged along the midline, left side extending farther forward than right side, margin straight; covers less than ½ the aperture. *Muscle scar:* large, ovate, anterior to the septum on the right side. *Sculpture:* fine growth lines only. *Color:* variable, from tan to purple; fine reddish lines visible on tan shells; Caribbean form (*C. navicula*): white background, brown spots. *Life history:* eggs large, yolky, 0.28 mm diameter (Conklin, 1897: 20); no pelagic larval stage. *Radula* (Fig. 24): central tooth formula: $\frac{3\text{-}1\text{-}3}{0\text{-}0}$ to $\frac{4\text{-}1\text{-}4}{0\text{-}0}$. Lateral: $\frac{3\text{-}1\text{-}7}{0}$ to $\frac{3\text{-}1\text{-}8}{0}$. Inner marginal: $\frac{7}{5}$ to $\frac{10}{6}$. Outer marginal: $\frac{5}{0}$ to $\frac{7}{0}$. *L. max.:* 18.5 mm (Recent). Over 200 specimens, over 50 localities. *L. max.:* 24.0 mm (fossil). Over 200 specimens, 8 localities.

Remarks:

Although *C. glauca* has page precedence, *C. convexa* was used by Verrill & Smith (1874) acting as first revisers and is the name established in the literature (Franz & Hendler, 1970). A controversy once existed over the validity of the name *C. glauca,* given to the large, flat form occupying uncurved substrates. *C. convexa* was originally named from specimens found on the shells of other gastropods (Dall, 1889a; Ford, 1889, 1890; Stone, 1892; Stearns, 1899). Dwarfs living on the blades of eel grass produce eggs at a size (4 mm long) at which most *C. convexa* are immature. Fossil specimens, especially those from the Miocene, attain significantly larger sizes than any Recent specimens.

C. acuta was named for a narrow substrate form. *C. navicula,* a spotted shell, convex and about 10 mm long, possibly also belongs here. Its anatomy and life history should be compared with the continental *C. convexa* to test the synonymy.

Crepidula costata Sowerby

C. costata Sowerby, 1824: fig. 3, descriptive letterpress (New Zealand).

C. costata Deshayes, 1830: 26. Non *C. costata* Morton, 1829 (no locality).

Distribution:

?Miocene: New Zealand (Suter, 1913)
?Pliocene: New Zealand (Suter, 1913)
Recent: New Zealand

Description:

Shell: moderately thick; convexity: 1.34; obliqueness: $9°$; aperture elongate, ovate, L/W: 1.53 (n = 20). *Beak:* almost directly posterior, not twisted, at shell margin; protoconch usually worn off, forming a blunt apex; beak small, does not extend beyond the aperture, not excavated. *Septum:* very shallow, planar; margin straight across with sides prolonged (like Fig. 2G), covers ½ the aperture. *Muscle scars:* large ovate scar in front of the right side of the septum, with earlier insertion points visible as a strip behind it. Another smaller muscle scar at the left corner of the septum. *Sculpture:* heavy radial corrugations on the shell, forming ribs. *Color:* brown lines of variable width following the radial corrugations, alternating with white rays; inside white. *Life history:* larvae planktonic. Breeds in February (Pilkington, 1974). *L. max.:* 43 mm; 35 specimens, 6 localities.

Remarks:

The name *Crepidula costata* has been used independently 3 times, twice to de-

scribe this New Zealand species. It was also used for a fossil related to *C. aculeata,* as discussed above (Morton, 1829). Deshayes' *C. lineolata* from Australia (Deshayes, 1830) could be synonymous, because he described an elongate, convex specimen of about the right size, color, and septal configuration. The type is not illustrated, and I have not had access to any specimens purported to be *C. lineolata.* Dall (1892) calls it an "unknown" species.

C. costata shares the characteristic of 2 muscle scars with only 4 other species, all from the Pacific Ocean. Its strongly plicate ribs are a part of its growth pattern regardless of substrate. I have seen no spinous specimens. Suter (1913) combined *C. aculeata* with *C. costata,* therefore his fossil records are questionable.

Crepidula cymbaeformis Conrad   Fig. 9

C. *cymbaeformis* Conrad, 1844: 173 (Petersburg, Virginia; Miocene). Syntypes: ANSP 15341.

C. *recurvirostra* Conrad, 1871: 78 (North Carolina; Miocene) [syn. nov.]. Syntypes: ANSP 20221.

C. *phalaena* Weisbord, 1962: 208, pl. 19, figs. 3-5, 16-18 (Mare Formation, Venezuela) [syn. nov.].

C. *avirostra* Weisbord, 1962: 209, pl. 19, figs. 6-7 (Mare Formation, Venezuela) [syn. nov.].

C. *corcovada* Weisbord, 1962: 211, pl. 19, figs. 8-10 (Mare Formation, Venezuela) [syn. nov.].

Distribution:

Miocene: Florida to North Carolina (including early stages of Yorktown, Duplin Formations)

Pliocene: Florida to North Carolina; Venezuela (Mare Formation) [Weisbord, 1962].

Pleist.: Florida to North Carolina (Caloosahatchee; Waccamaw Formations)

Description:

Shell: moderately thick; convexity: 1.34; obliqueness: 20°; elliptical and tapering at both ends of the aperture, L/W: 1.68 (n = 20). *Beak:* Slightly inclined, rostrate, at the level of the shell margin, extending beyond

the aperture posteriorly, not excavated. *Septum:* shallow, concave, covering ½ the aperture; margin deeply notched at the corner (V-shaped). *Muscle scar:* none visible. *Sculpture:* only very fine growth lines. *L. max.:* 41.5 mm; 25 specimens, 5 localities.

Remarks:

C. recurvirostra fits this species description in all details. Weisbord's species are growth forms, *C. corcovada* having grown on a ribbed surface. Dall (1892: 357) and others did not consider *C. cymbaeformis* unique enough to be a species distinct from *C. fornicata,* but I find it readily distinguishable and common in the Pliocene. It is rare in the Pleistocene. There is no comparable species in size and shell characters living in the Western Atlantic today, but it can be compared ecologically with the modern *C. norrisiarum* of the Eastern Pacific as it is of comparable size and shape, intermediate between *C. fornicata* (or *C. onyx*) and *C. convexa* (or *C. adunca* in the Pacific).

Crepidula densistriata Suter

C. *densistriata* Suter, 1917: 10, pl. 2, fig. 11 (Awamoa beach and creek, North Otago Miocene, New Zealand). Holotype: New Zealand Geol. Surv.

Distribution:

Miocene: North Otago, New Zealand

Description (based on original description and illustration):

Shell: ovate, oblique; body whorl laterally compressed. *Beak:* incurved, turned to the right, slightly rostrate. *Septum:* not visible on type material. *Muscle scar:* not visible on type material. *Sculpture:* fine, radial striation; fine concentric growth lines. *Color:* unknown. *L:* 28 mm; *H:* 13 mm (holotype).

Remarks:

This species is similar to *C. incurva* (Broderip). It is unlike any other Miocene Indo-Pacific species due to its sculpture and oblique growth form.

Crepidula dilatata Lamarck

C. *dilatata* Lamarck, 1822: 25 (Barbary [Northern Africa]). Type in the Geneva Museum, fide Mermod, 1950: 724.

C. *subspirata* de Blainville, 1824: 295, pl. 48, fig. 7 (no locality).

Calyptraea adolphei Lesson, 1830: 388, pl. 15, fig. 2 (Talcahuano, Chile).

Crepidula depressa Deshayes, 1830: 26 (Chile).

?C. *patula* Deshayes, 1830: 27 (coast of Tahiti) [fide Carpenter, 1857a: 272].

C. *nautiloides* Lesson, 1832: 2 p., pl. 42, figs. 1-3 ("Pacific Ocean?").

C. *capensis* Quoy & Gaimard, 1832-33: 424, pl. 72, figs. 13-14 (Cape of Good Hope; New Holland [Southern Africa]) [syn. nov.].

Calyptraea strigata Broderip, 1834: 39; 1835: 203, pl. 28, fig. 12 (Valparaiso, Chile).

C. *pallida* Broderip, 1834: 39; 1835: 204, pl. 29, fig. 3 (Falkland Islands).

Crepidula peruviana Deshayes, 1836: 49 (Island of San Lorenzo, Peru). Type in the Geneva Museum, fide Mermod (1950: 726).

C. *patagonica* d'Orbigny, 1841: 464; 1846, pl. 58, figs. 1-3 (Patagonia).

C. *rugulosa* Dunker, 1846: 108 (Cape of Good Hope) [syn. nov.]. Type in Berlin Museum of Natural History.

C. *dilatata* Lamarck. Carpenter, 1857a: 272; Brann, 1966, tablet 1353.

C. *uncinata* Philippi, 1887: 94, pl. 11, fig. 6 (Tertiary of Chile).

Crypta subdilatata Rochebrune & Mabille, 1889: 37 (Cape Horn).

Crepidula dilatata Lamarck. Ortmann, 1902: 185, pl. 32, fig. 11.

Distribution:

?Oligocene: Argentina (Cape Fairweather) (Ortmann, 1902)

U. Miocene: Araucano strata, Argentina (Parodiz, 1939)

Pleist.: Argentina and Chile (von Ihering, 1907)

Subrecent: Southern Chile and Argentina (Parodiz, 1939)

Recent: Americas: Buenos Aires to Cape Horn to Mazatlan, Mexico (museum records). Central West and South Africa (Dunker, 1846). "Sandwich Islands" (Museum records; exact locality unknown)

Description:

Shell: moderately thick to thick, large, globose; convexity: 1.52; obliqueness: 10°; aperture circular: L/W: 1.19 (n = 30). *Beak:* small, turned to the right and slightly upturned, appressed to body whorl above the aperture; not excavated; barely extends posteriorly beyond the aperture; very high whorl expansion rate. *Septum:* shallowly inserted but strongly concave, thin, undulating with a deep sinus at the left side of the shell and a small median notch; ridged along the midline in young specimens; covers less than ½ the aperture. *Muscle scar:* deep, small, lunar; under right anterior corner of septum. *Sculpture:* only growth lines. *Shell color:* white, or white mottled with brown inside the shell; outside tan or brown, often with radial brown lines visible at the shell margin. *L. max.:* 59 mm; about 100 specimens, 26 localities.

Remarks:

This common species can possess permanent indentations on the shell caused by stacking. The center of its current distribution is southern Chile. Like C. *grandis,* with which it has been confused, C. *dilatata* is robust and inflated, but it differs markedly in conformation of beak and septum. It is allied to the smaller, more delicate C. *dorsata* on the basis of these characters. In fact, both have been placed in a subgenus, or even genus, *Crepipatella* Lesson, due to the form of the septum, intermediate between *Crepidula* and *Crucibulum.* The Tertiary C. *gregaria* overlapped in space and time with C. *dilatata.*

C. *patula* from Tahiti probably belongs under C. *dilatata,* although I have not examined type material and the original description is without illustration. The forms which Broderip named represent slight differences in shell shape and color; *Calyptraea* (= *Crepidula*) *strigata* has a distinct white ray along the mid-dorsal line. C. *pallida* is a white-shelled form. D'Orbigny's C. *patagonica* is also a growth variant, as is C. *depressa* (flattened). C. *rugulosa* and C. *capensis* are slightly spinous variants. *Calyptraea adolphei, Crepidula nautiloides,* C. *peruviana,* and *Crypta subdilatata* are obvious synonyms.

Crepidula diminutiva Loel & Corey

- *C. diminutiva* Loel & Corey, 1932: 267, pl. 63, figs. 13-15 (Upper Vaqueros Formation, L. Miocene, California, Orange County). Holotype: U. Calif. Coll. Invert. Paleo. 31574.
- *C. bractea* Addicott, 1970: 62, pl. 4, figs. 5-7, 15-17 (Upper Olcese Sand, Middle Miocene, California). Holotype: USNM 650088. [syn. nov.].

Distribution:

L. Miocene: Southern California, Orange County to Santa Barbara
M. Miocene: Kern River, California (Addicott, 1970)

Description (Based primarily on illustrated specimens; 3 specimens observed)

Shell: small, thin, convexity low, right side of shell nearly perpendicular to the aperture; subelliptical to nearly circular. *Beak:* small, forming one whorl; nearly bilaterally symmetrical; appressed to shell at or near the margin; not excavated; not rostrate. *Septum:* thin, shallow, planar; covers about ½ the aperture; margin unknown. *Muscle scar:* 1 visible. *Sculpture:* none except fine but irregular growth lines. *L. max.:* 17.0 mm. 3 specimens, 2 localities.

Remarks:

C. bractea was thought to differ from *C. diminutiva* in apertural outline and in convexity, but these are both plastic characters under some degree of environmental influence. The largest specimen (16.5 mm) of *C. diminutiva* which I observed is distinct from other fossil Californian *Crepidula* species in being nearly bilaterally symmetrical but not rostrate. The small number of shells extant may be due to their fragility.

Crepidula dorsata (Broderip)

- *Calyptraea dorsata* Broderip, 1834: 38; 1835: 202, pl. 28, fig. 10 (St. Elena [Ecuador]).
- *Crepidula lingulata* Gould, 1846: 160 (Puget Sound) [syn. nov.]. Holotype: USNM 5871.
- *C. bilobata* Reeve, 1859 (ex Gray ms.): pl. 5, fig. 29 (no locality). Type in BM(NH).
- *C. dorsata* (Broderip). Carpenter, 1864: 654.
- *C. fissurata* Sowerby, 1883: 67, pl. 9, fig. 151 (no locality). Type in BM(NH).
- *C. orbiculata* Dall, 1919: 351 (Vancouver, Canada) [syn. nov.]. Type in USNM.
- *Crepipatella fluctuosa* Taki, 1938: 144, figs. 6-7 (Wakayama, Japan) [syn. nov.].

Distribution:

Pliocene: Los Angeles to Santa Barbara, California (Grant & Gale, 1931)
Pleist.: Baja California to Los Angeles, California (Woodring et al., 1946)
Recent: Valparaiso, Chile, to Vancouver; South Bering Sea; E coast of Japan (8° to 60° N. Lat.—Keen, 1937, after Dall, 1921). Especially in areas of cold upwelling. Distribution patchy.

Description:

Shell: small, thin; convexity: 1.24; obliqueness: 12°; aperture subcircular; L/W: 1.02 (n = 50). *Beak:* small, twisted strongly to the right, far above the aperture, apex free from shell (slightly rostrate); not excavated, not extending beyond the aperture. *Septum:* shallow, concave, bilobed, freed from the entire left side of the shell by a deep sinus; strong central notch also. Ridged along the midline. Septum covers about ¼ of the aperture. *Muscle scar:* absent. *Sculpture:* growth lines (often undulating); occasional crenulations of the shell margin due to substrate texture. *Shell color:* white to yellow; tinged, spotted, or rayed with chestnut; inside white or purplish. *Life history:* planktonic larval stage; egg diameter = 0.15 mm (Coe, 1949). *L. max.:* 26 mm; over 200 specimens, 34 localities.

Remarks:

An erroneous range in northern Alaska was given by Dall (1921) who confused *C. grandis* with this species. *C. dorsata* is nonetheless widely distributed, covering the length of the Eastern Pacific coast, thriving

in deep water (20 m is a common depth on museum labels) or in areas of cold upwelling.

Broderip's figured specimen shows ribbing. *C. bilobata* is a chestnut-rayed color form. Stating no reason, Keen (1971) and Grant & Gale (1931) consider *C. lingulata* a valid species name and dispute its synonymy with *C. dorsata.* Smith (1946) breaks the group into a southern species (*C. dorsata*) and a northern one (*C. lingulata*), solely on the basis of latitude. Many *Crepidula* species have wide latitudinal ranges, extending across zoogeographic "boundaries," and I can find no consistent character to separate these 2 supposed species.

C. orbiculata Dall is a white form with strongly twisted beak (more than one complete whorl), and is found in deep, cold water (Vancouver). *C. fissurata* is irregularly shaped, much like *C. orbiculata,* but with purple pigment stains inside. Another name, *Verticumbo charybdis* Berry (1940), was erected for a similar but even more coiled shell found in deep water off Southern California. Topotypes (MCZ 174626) have large, calyptraeid-like apices and ribs, as in *Trochita sordida* Broderip (1835). I would not synonymize *V. charybdis,* but point out the morphological parallels. Berry claims that the septum is less indented than in *C. lingulata* (= *dorsata*), and that its free edge is upturned. Deep water populations are affected by different physical conditions than are shallow populations, and are isolated as adults due to patchiness of suitable substrate. Both environmental and genetic factors may cause variation in the above traits. More specimens of the form named by Berry should be examined to determine if it is a genuine species, perhaps of *Calyptraea.* A Japanese form of *C. dorsata,* named *Crepipatella fluctuosa,* is irregularly ribbed.

C. aculeata is similar to the "Crepipatella" group in size and beak characters, and its septum is deeply notched at the left and at the center, resembling the bilobed *C. dorsata.*

Crepidula excavata (Broderip)   Fig. 10

> *Calyptraea excavata* Broderip, 1834: 40; 1835: 205, pl. 29, fig. 7 (Real Llejos, Chile). Syntypes: BM(NH) 1966637.
> *C. arenata* Broderip, 1834: 40; 1835: 205, pl. 29, fig. 8 (St. Elena, "West Columbia" [syn. nov.]. Holotype: BM(NH) 1966631.

> *Crepidula excavata* (Broderip). Deshayes, 1836: 649 (Chile).
> *C. excavata* (Broderip). Reeve, 1859: pl. 1, fig. 4.
> *C. excavata* (Broderip). Carpenter, 1857a: 274.

Distribution:

?Pleist.: San Quintin Bay, Baja California, to Santa Monica Palisades, California (Grant & Gale, 1931)

Recent: Chile (Deshayes, 1836); 3° 28' S. latitude (Peru) to San Felipe, Baja California (SDNHM)

Description:

Shell: large, thick; convexity: 1.36; obliqueness: 34°; prominent, angular dorsal arch; aperture elliptical, narrowed at either end; L/W: 1.56; left side of shell compressed (n = 30). *Beak:* pointed, turned to the right and hooked; at the level of shell margin but free from it; early portion of shell does not extend beyond the aperture; beak often excavated. *Septum:* deeply inserted, planar or slightly convex, margin slightly undulating and diagonal, attached farther forward on the left side. Covers $\frac{1}{3}$ to nearly $\frac{1}{2}$ of the aperture. *Muscle scar:* large, deep, chevron-shaped; on right side and in front of the septum. *Sculpture:* only growth lines. *Shell color:* yellowish to light brown maculation on white, or reddish brown radial streaks and white rays; pale tan or white inside; thin tan periostracum. *L. max.:* 52 mm. 70 specimens, 8 localities.

Remarks:

According to Chace (1916: 35), this species has "an evenly curved deck extending forward on both sides." As can be seen from Broderip's figure, this is incorrect. He clearly shows the diagonal septum, related to the highly oblique growth of the shell, and the striking muscle scar. The muscle scar is the largest I have observed in *Crepidula* relative to the size of the shell. Several malacologists (e.g. Keen, 1971) have used the excavated beak to separate this from other species, but it is absent in shells which have grown unrestricted on flat substrates. Furthermore, other California species also have this character, e.g. *C. adunca.*

Broderip's *Calyptraea* (= *Crepidula*)

arenata is a young, flat specimen of *C. excavata.* Most museum specimens labeled "*C. arenata*" are *C. excavata,* while many of those labeled "*C. excavata*" are in reality the *C. naticarum* of Williamson (1905). Berry (1950) claims that *C. arenata* has a deeply impressed muscle scar and that *C. excavata* does not; this is contrary to Broderip's original intent. Dall (1909b) thinks *C. arenata* to be a variant of *C. onyx.* Coe (1949) states that *C. arenata* has an egg diameter of 0.16 mm and a planktonic larval stage, but it is not clear what species he had. It is surprising that so much confusion could exist over *C. excavata,* which is one of the most distinctive species of *Crepidula.* Because Grant & Gale (1931) did not illustrate their supposed Pleistocene *C. excavata,* I cannot be sure that their reference is to the true *C. excavata.* Woodring et al. (1946) cite *C. excavata* from the Pleistocene of Palos Verdes, California but the species they describe is *C. norrisiarum.*

Some African specimens labeled *C. lentiginosa* Sowerby, 1883, are identical with *C. excavata,* at least in shell morphology. There are 2 entities called *C. porcellana* (Linnaeus, 1758) from Africa in museum collections, 1 of which is hardly distinguishable from *C. excavata* and the other of which resembles *C. hepatica* Deshayes, 1830. Resolution of the synonymy will depend on examination of the African types; that of *C. porcellana* may be lost, for it is not among the "*Patella*" in the Linnaean Society Collection. Equality of these species would create an unusual geographical distribution. *C. maculosa* from the Gulf of Mexico and northern Caribbean is intermediate geographically, and is similar in muscle scar and color pattern to *C. excavata* and the African species, but is smaller.

C. excavata lives primarily offshore and is dredged in depths to 100 m.

Crepidula fornicata (Linnaeus)   Fig. 11

   Patella fornicata Linnaeus, 1758: 781 (ad Ilvam insulam [Elba Is., Mediterranean Sea]). Locality in error. Type: Linnaean Society, London.
   Crypta nautarum Mörch, 1877 [ex Humphrey, 1779 (ruled invalid by ICZN)] : 103 (North America).
   Patella fornicata Linnaeus. Gmelin, 1791: 3693 (Barbados, "Iliam," and elsewhere in the Mediterranean).

   Crepidula fornicata (Linnaeus). Lamarck, 1822: 24 (Barbados).
   Crypta densata Conrad, 1843: 311 (Natural Well, Duplin Co., North Carolina; Miocene). Syntypes: ANSP 15321.
   ?Crepidula riisei Dunker, 1852: 189 (San Juan, Puerto Rico) [fide Tryon, 1886]. Type lost.
   C. fornicata (Linnaeus). Conrad, 1861: 81, pl. 45, fig. 10.
   C. virginica Conrad, 1871: 78 (Virginia; Miocene). Syntypes: ANSP 30707.

Distribution:

?Oligocene:	Calhoun Co., Florida (juveniles only)
Miocene:	Florida to Nantucket (Choctawhatchee, Duplin, Yorktown Formations)
Pliocene:	Florida to New Jersey (late stages of Yorktown, possibly Duplin Formation)
Pleist.:	Florida to Nantucket (Waccamaw, Caloosahatchee Formations)
Recent:	Progreso, Mexico; Long Island, Bahamas to Port Aransas, Texas; North to Prince Edward Island. Introduced, Washington State; S England to S Norway. Rarely, St. Thomas, Virgin Islands, and possibly elsewhere in the Caribbean.

Description:

Shell: shape highly variable; convexity: Recent, 1.54; Miocene, 1.73; obliqueness: Recent, 18°; Miocene, 34°; L/W: Recent, 1.42; Miocene, 1.55. Aperture elliptical (n = 50). *Beak:* blunt, turned to the right and appressed to the shell margin or slightly above it; not highly coiled; not excavated; can extend beyond aperture posteriorly and laterally if shell grows on a restricted substrate. *Septum:* concave, rather shallow, weakly notched at the left side and in the center; occupies about ½ the aperture (more in some Miocene specimens); is attached slightly farther forward on the right side. *Muscle scar:* absent. *Sculpture:* growth lines only. *Shell color:* white and brown alternating rays, usually with a broad white ray along the dorsal midline; pigment intensity highly variable; interior tan to purple; brown ring around the white septum. *Life history:*

small eggs of diameter 0.16-0.18 mm; planktonic larval stage. *Radula* (Fig. 24): central tooth formula: Martha's Vineyard: $\frac{9-1-9}{0-0}$ (serrated); to $\frac{10-1-11}{0-0}$; Nahant: $\frac{2-1-2}{0-0}$ to $\frac{3-1-3}{0-0}$. Inner marginal: $\frac{6}{3}$ to $\frac{7}{9}$. Outer marginal: $\frac{2}{0}$ to $\frac{7}{0}$ (not illustrated). Lateral: $\frac{4-1-5}{0}$ to $\frac{4-1-7}{0}$. *L. max.:* 59 mm (Recent); 65 mm (fossil). Over 200 specimens, over 200 localities.

Remarks:

Linnaeus followed Gualtieri (1742) for his type-locality "ad Ilvam insulam," in the Mediterranean Sea. He did not know the locality of the actual specimens in his collection. Dezallier d'Argenville (1742, pl. 6, fig. N) and Lister (1770, pl. 545, figs. 33, 35), also referred to by Linnaeus, represent the true *Crepidula fornicata* as we know it today; Lister was first with the locality "Barbados." Gmelin's 13th edition corrected Linnaeus' error by removing the reference to Gualtieri, whose figure is ambiguous but is probably of *C. unguiformis.* Part of the confusion is due to a similar species, *C. gibbosa* from the Mediterranean Sea.

When *Crepidula fornicata* was introduced into northern Europe on oysters at the turn of the century, it became established as a major faunal element. *C. gibbosa* has not similarly spread, nor does it tend to form large stacks as does *C. fornicata.*

Shells identical to modern *Crepidula fornicata* occur in the Miocene of North Carolina (Duplin and Yorktown Formations). However, this species was even more variable in the Miocene than it is today (Fig. 11). The degree of beak coiling (representing whorl expansion rate early in ontogeny and asymmetry of growth) and the length of the septum relative to the aperture were two notably unstable characters of that period. Also, the Miocene fossil specimens have a slightly larger maximum and median size than do Recent specimens. *Crypta densata* was a massive form, and *Crepidula virginica* a highly coiled form. An illustration by Sowerby in Reeve (1859, pl. 3, fig. 15b) includes a prominent muscle scar; this is erroneous.

It is surprising that there are so few synonyms for such a variable species. On the contrary, many valid species such as *Crepidula maculosa* and *C. plana* have at one time or another been synonymized under *C. fornicata* (Dall, 1892). Dunker named *C. riisei* from San Juan, Puerto Rico; the type is lost from the Berlin Museum, so Tryon's opinion cannot be verified. Reference to concavity in the original description suggests that the snail may have been *C. plana.* Reeve (1859) mistakenly used the name *C. nautiloides* for narrow, stacked specimens of *C. fornicata* from New York. Philippi (1836)

FIG. 10. *Crepidula excavata* from Baja California, 5 views; a) dorsal, L = 41.1 mm; b) ventral, L = 38.4 mm; muscle scars were accentuated by coating the shell with magnesium oxide; c) lateral, L = 39.8 mm; d) posterior, showing the oblique angle of the shell; W = 26.9 mm; e) anterior, showing the beak; same specimen as d.

FIG. 11. *C. fornicata* from North Carolina Miocene, 3 views; a) dorsal, L = 32.0 mm; b) ventral, L = 31.0 mm; c) lateral, L = 31.6 mm.

FIG. 12. *C. gibbosa* from Italy, fossil and Recent, 3 views; dark spots are holes, not muscle scars; a) dorsal, fossil, L = 31.4 mm; b) ventral, same specimen; c) ventral, Recent, L = 23.0 mm; d) lateral, same specimen as a and b.

FIG. 13. *C. immersa* from South Australia, 3 views; a) dorsal, L = 22.0 mm; b) ventral, L = 33.9 mm; c) lateral, same specimen as a.

FIG. 14. *C. monoxyla* from New Zealand, 3 views; a) dorsal, L = 28.0 mm; b) ventral, same specimen; muscle scars have been accentuated with ink lines. c) lateral, same specimen.

FIG. 15. *C. marginalis* from Panama (Pacific), 3 views; a) dorsal, L = 22.4 mm; b) ventral, same specimen; c) lateral, same specimen.

FIG. 16. *C. onyx* from Southern California, 3 views; a) dorsal, L = 55.4 mm; b) ventral, same specimen; c) lateral, same specimen; this specimen, taken from a rock, is less arched than those which stack upon one another.
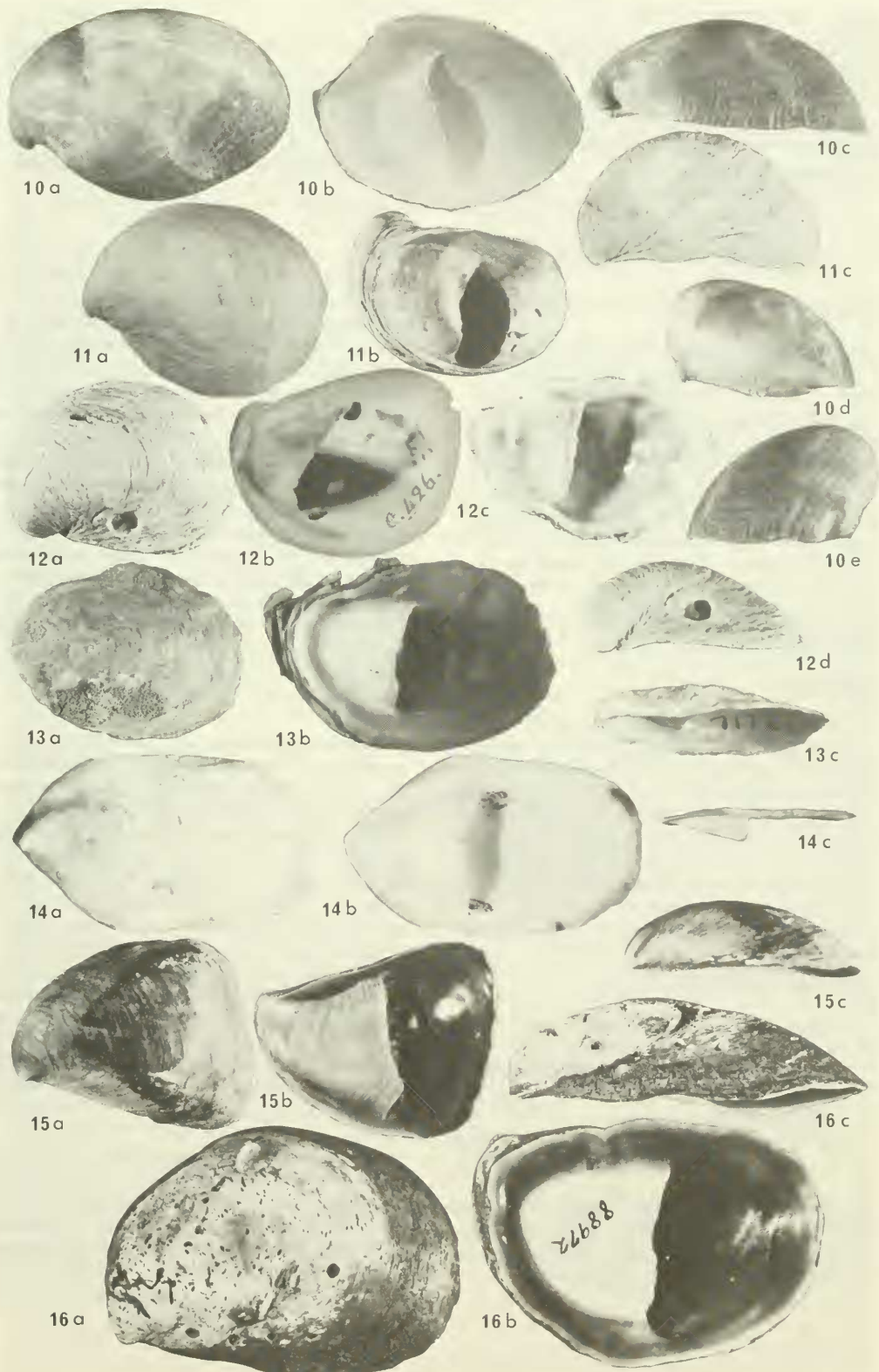
erred by identifying *C. gibbosa* as *C. fornicata.*

The radula variations between Nahant and Martha's Vineyard are striking, but are based on only a few specimens. Still, these data show the danger of characterizing a species on the basis of one or a few radulae.

Crepidula gaultina Buvignier

> *C. gaultina* Buvignier, 1852: 28, pl. 21, figs. 29-30 (Varennes, France; Gault, Cretaceous); 1864, in Pictet & Campiche: 694, pl. 97, figs. 3-4.

Distribution:

Cretaceous: Varennes, France (rare); St. Croix, Virgin Islands (rare)

Description: (from illustrations and descriptions by Buvignier):

Shell: convex, not oblique but nearly symmetrical about the apex; aperture elliptical. *Beak:* small, slightly rostrate, above the apertural plane; not twisted. *Septum:* seen only as a slit in the internal molds. *Muscle scar* and *Sculpture:* not seen on material available. *L. max.:* 18 mm.

Remarks:

This species is known only from internal molds, but an internal septum is evident. This is 1 of only a few really convincingly classified Cretaceous *Crepidula* species, if the stratigraphy is accurate. There are a few records of the genus *Calyptraea* from the same St. Croix locality. In the Cretaceous, the St. Croix and Varennes localities were close together.

Crepidula gibbosa Defrance   Fig. 12

> *C. gibbosa* Defrance, 1818: 397 (Touraine, France; Miocene).
> *C. moulinsii* Michaud, 1829: 265, fig. 9 [suggested by Saussaye, 1869: 96] (Mediterranean Sea).
> *C. gibbosa* Defrance. Deshayes, 1836: 647 (Touraine and Laugnan near Bordeaux, fossil).
> *C. pulchella* Aradas, 1846: 176 [fide Saussaye, 1869: 96]. Type at Catania.
> *C. moulinsii* Michaud. Bucquoy et al., 1886: 462, pl. 5, figs. 12-14.

Distribution:

Miocene: Vienna Basin; Touraine, France; Italy
Pliocene: Calabria, Italy
Pleist.: Monte Pellegrino; scattered other S. European localities
Recent: Mediterranean Sea; Adriatic Sea

Description:

Shell: thick; convexity low: 1.20; obliqueness: 12°; aperture ovate but variable; L/W: 1.29 (Miocene specimens, n = 15). *Beak:* very slightly inclined and appressed to, or at shell margin; pointed; not excavated; does not extend beyond aperture. *Septum:* shallow, concave, margin nearly straight, covering $1/3$ of the aperture; square notch at left side. *Muscle scar:* absent. *Sculpture:* none except fine growth lines; often, roughness due to calcium carbonate deposits on dorsal surface. *Shell color:* chestnut-colored exterior; variable in intensity to nearly white; light tan inside, and very porcelaneous. *Life history:* not reported; stacking does not occur. *L. max.:* 32 mm; over 200 specimens, 20 localities (fossil and Recent).

Remarks:

Crepidula gibbosa was named from fossil specimens; an identical living organism from the same geographical area was later named *Crepidula moulinsii*. Vayssière's (1893) illustrated specimens of *C. moulinsii* appear to be juveniles and are of little use distinguishing this species. *C. gibbosa* is similar to *C. fornicata*; however, it never reaches the size of the latter species and is never highly arched. The *C. "fornicata"* of Costa (1829) and Philippi (1836), and other reports of *C. fornicata* from the Mediterranean, really are *C. gibbosa.* Editions of the *Systema Naturae* which give localities for *C. fornicata* of Barbados and the Mediterranean are based on mixed specimens of *C. fornicata* and *C. gibbosa.*

Crepidula grandis Middendorff   Fig. 23

> *C. grandis* Middendorff, 1849a: 101, pl. 11, figs. 8-10 (St. Pauls Is., Bering Sea); 1849b: 18. Type: Academy of Sciences, Leningrad.

C. grandis Middendorff. Taki, 1938: 145, fig. 1.

Distribution:

Recent: Arctic Sea, Bering Strait, Alaska; Kamchatka; Siberia; Kuril Is.; N Japan (museum records). (Keen, 1937: 57°-72° N. Lat.; but Kuroda & Habe, 1952: 36°-46° N. Nat. in Asian waters.)

Description:

Shell: moderately thick to thick; convexity: 1.54; obliqueness: 16°; aperture round to ovate; L/W: 1.35 (n = 20). *Beak:* small, twisted strongly to the right and upturned to lie above the shell margin but not appressed to it; one full whorl is completed before expanding into adult portion of shell; beak not excavated, extends posteriorly beyond the aperture. *Septum:* deeply recessed, slightly convex, margin straight, diagonal, attached quite far forward on the left side, covers half the aperture. *Muscle scar:* deep, rectangular, forward of right corner of septum. *Sculpture:* only coarse growth lines. *Shell color:* white inside, light tan to red outside. Thick brown periostracum. *L. max.:* 57 mm; 24 specimens, 6 localities.

Remarks:

This species has been synonymized with the southern hemisphere species *C. dilatata* (Tryon, 1886) incorrectly, giving an incorrect range for the latter species. Grant & Gale (1931) consider *C. grandis* to be a direct descendant of the fossil *C. princeps*, but Woodring et al. (1940: 71) disagree. According to paleontological evidence, *C. princeps* died out in the northern part of its range before *C. grandis* appeared. On the basis of muscle insertion and septum shape, *C. grandis* does have affinities with the fossil species, although it is never as large and tends to be less elongate, with a proportionately narrower beak. To say that *C. grandis* is a direct linear continuation of *C. princeps* as did Grant & Gale (1931) is overstepping the evidence. It may be related to a northern group of *C. princeps* which became isolated as the species' range contracted, becoming able to survive the conditions which eliminated its relatives.

Crepidula gregaria Sowerby

C. gregaria Sowerby, 1846: append., p. 254, pl. 3, fig. 34 (Patagonia; Pleistocene) [spelled *gregarea* in error, but *gregaria* in plate caption].

C. gregaria Sowerby. Philippi, 1887: pl. 12, fig. 1.

Distribution:

Pleistocene: Patagonia and southern Chile

Description (based on the literature):

Shell: highly convex; obliqueness and L/W not measured but similar to those of *C. fornicata*; aperture elliptical. *Beak:* blunt, turned to the right and appressed to the shell margin; not excavated; extends beyond the aperture laterally. *Septum:* bisinuate margin (Finlay, 1924). *Muscle scar:* unknown. *Sculpture:* growth lines only. *Shell color:* unknown. *L.:* 35 mm (Philippi, 1887).

Remarks:

This fossil from the Quaternary of Patagonia and southern Chile is remarkably similar to *C. fornicata* in size and beak characters. It was preserved *in situ* in stacks within gray argillaceous sandstone, hence the name. A long distance with isolating currents separated the North American Atlantic and the South American Pacific during the Tertiary, making it difficult to believe that *C. gregaria* was the same as the North American species. No Recent species is in both of these zoogeographical provinces. At the least, *C. fornicata* and *C. gregaria* are closely allied in morphology, habitat, and life history characters as inferred by the stacking. *C. gregaria* also is similar in general form and habitat to *C. princeps* of the West Coast of North America. I have not examined specimens of *C. gregaria* personally; a look at its septum (described as "bisinuate" in the literature) and its maximum size would clarify its affinities.

Crepidula haliotoidea Marwick

C. haliotoidea Marwick, 1926: 318, pl. 73, fig. 10 (Tirangi Stream, N. Taranaki, New Zealand; Upper Miocene). Type in New Zealand Geological Survey collection.

Distribution:

Upper Miocene: Northern New Zealand

Description (based on original description and illustration):

Shell: moderate in size, ovate. *Beak:* directed upward, above the margin, forming ½ whorl; oblique, not rostrate, not appressed. *Septum:* covers ½ the aperture; concave margin in early stages (edge of septum not visible in specimens described). *Muscle scar:* unknown. *Sculpture:* only coarse growth ridges. *Shell color:* unknown. *L.* of holotype: 37 mm.

Remarks:

This shell is similar in shape to a *Haliotis,* for which it was named. It closely resembles the much older *C. hochstetteriana.*

Crepidula hochstetteriana Wilckens

> *C. hochstetteriana* Wilckens, 1922: 5, pl. 1, fig. 9a,b (Lower Amuri Group, E. and W. wing of Amuri Bluff, New Zealand; Cretaceous).

Distribution: as above

Description (based on original description and illustrations):

Shell: ovate, left side convex, right side concave; nearly twice as long as wide. *Beak:* curved to the right, extending slightly beyond the margin; not rostrate. *Septum:* covers nearly ½ the aperture; margin concave. *Muscle scar:* unknown. *Sculpture:* only coarse, wrinkled growth lines. *L.:* 49 mm; *W:* 26 mm; ht: 22 mm (holotype).

Remarks:

The species is known from internal molds, as are all Cretaceous *Crepidula* species. The septum is clearly indicated. Only a few specimens have been found.

Crepidula immersa Angas   Fig. 13

> *C. immersa* Angas, 1847: unnumbered plate with descriptive letterpress (South Australia).

Distribution:

Recent: Southern Australia

Description:

Shell: thin, nearly planar; convexity: 1.05; obliqueness: 2°; spatulate; L/W: 1.53 (n = 5). *Beak:* protoconch tiny; nearly backward, free from shell; at the level of the margin, extending just beyond it; not excavated. *Septum:* very shallow; planar or convex; very short, covering about ¼ of aperture; margin undulatory with a very shallow notch at the left side. *Muscle scar:* shallow, small, at right corner of septum; a small pit can be present at left corner. *Sculpture:* none except fine growth lines. *Shell color:* tan or white exterior; brown interior. *L. max.:* 42.5 mm; 5 specimens, 3 localities.

Remarks:

This species is distinctive by its coloration and very short septum. It is 1 of the convergent planar forms of *Crepidula* occupying sheltered, hard substrates. It and *C. monoxyla* are the only such *Crepidula* species with muscle scars; *C. immersa* is the only planar *Crepidula* with consistently dense pigmentation.

Crepidula incurva (Broderip)

> *Calyptraea incurva* Broderip, 1834: 40; 1835: 204, pl. 29, fig. 6 (St. Elena & Xipixapi, "West Columbia"). Syntypes: BM(NH) 1966627. Non *C. incurva* Zittel, 1864.
>
> *Crepidula incurva* (Broderip). D'Orbigny, 1843: 468.
>
> *C. costulata* Dunker, 1852: 190 (Panama). Syntypes in Berlin Museum [syn. nov.] .
>
> ?*C. cerithicola* C. B. Adams, 1852: 225 (Taboga, Panama). Lectotype: MCZ 186293; paratype: MCZ 186294 [syn. nov.] .
>
> *C. incurva* (Broderip). Carpenter, 1857a: 276.
>
> *C. lirata* Reeve, 1859: pl. 5, fig. 30 (California). Types in BM(NH) [syn. nov.]. Non *C. lirata* Conrad, 1833.

Distribution:

Pleist: Canal Zone, Panama

Recent: Paita, Peru to San Felipe, Baja California

Distribution:

Eocene: Alabama; Louisiana (Gosport Sand).

Description:

Shell: small, laterally compressed; convexity: 1.34; obliqueness: 5°; L/W: 1.47 (n = 9). *Beak:* rostrate, directed nearly posteriorly, at the level of the shell margin or just above it, not excavated. *Septum:* deeply inserted, concave or planar, margin slightly curved inward, extending farther forward on the right side, covers ½ the aperture, sides do not extend forward. *Muscle scar:* absent; roughness from muscle attachment is on underside of septum at right corner. *Sculpture:* fine riblets on beak and over entire shell, unless worn. *Shell color:* outside: fine brown lines on solid tan or brown; inside darker brown; septum white; edge of shell brown and white, variegated. *Life history:* brooded development of lecithotrophic eggs (personal observation of dried specimens). *L. max.:* 25 mm; 9 specimens, 2 localities.

Remarks:

The fine ribbing of the shell is regular and consistent. The septum is quite different from that of *C. adunca,* which this species resembles in size and habitat. In color, muscle attachment, and septum configuration, *C. incurva* resembles *C. onyx.* The illustration of *C. lirata* in Reeve (1859) is representative of *C. incurva.* Dunker's *C. costulata* and Reeve's *C. lirata* are simple synonyms. *C. incurva* lives intertidally to at least 20 m.

The small shells named *C. cerithicola* by C. B. Adams have been thought to be *C. onyx* by many authors (e.g. Dall, 1909b) but I question this after examining Adams's types alongside juvenile *C. onyx.* The Adams specimens are worn, but are rayed with contrasting brown and white streaks, do not have a heavy periostracum, and do not have a dark interior. They may be *C. incurva.*

Crepidula lirata Conrad

- *C. lirata* Conrad, 1833: 344 (Claiborne, Alabama; Eocene). Lectotype: ANSP 15343. Non *C. lirata* Reeve, 1859.
- *C. cornu-arietis* I. Lea, 1833: 97, pl. 3, fig. 77 (Claiborne, Alabama; Eocene).
- *C. dumosa* Conrad, 1835: 46, pl. 16, fig. 20 (Claiborne, Alabama; Eocene). Holotype: ANSP 15302.

Description:

Shell: moderately thick; high convexity: 1.70; high obliqueness: 32°; width variable; L/W: 1.86 (n = 50). *Beak:* strongly inclined to the right, forming about 1 whorl; rostrate; above the aperture (distance above is variable); occasionally excavated; extends beyond the aperture laterally and posteriorly. *Septum:* deeply inserted, planar, covering ½ the aperture; margin straight or gently curved. *Muscle scar:* small, faint, lunar; at right corner of shell where it adjoins the septum. Not visibly impressed on all specimens. *Sculpture:* fine to coarse axial ribbing; fine growth lines. *L. max.:* 50 mm; over 200 specimens, 2 localities.

Remarks:

Shell markings show that *C. lirata* formed pairs, but none were preserved in situ, so whether it also formed stacks is unknown. The acute angle of the shell may have made stacks unwieldy. *C. lirata* is the major component of 1 layer of the Gosport Sand. It is the earliest preserved Eastern Coastal Plain species, but this does not imply that it is an early or "primitive" form of *Crepidula.* Its septum shows no likeness to that of early calyptraeid stock. The muscle scar is a character indicating migration of the muscle attachment to a position more effective for limpet-like existence.

C. cornu-arietis is a straightforward synonym; *C. dumosa* was named for 1 of the occasional specimens with short plicate spines on some (usually alternating) ribs.

Crepidula maculosa Conrad

- *C. maculosa* Conrad, 1846: 26 (Mullet Key, Tampa Bay, Florida). Non *Patella maculosa* Gmelin, 1791, which is not a *Crepidula,* but has been incorrectly equated with *C. maculosa.*
- *C. maculosa* Conrad. Stingley, 1952: 83, pl. 2, figs. 7-10.
- *C. maculosa* Conrad. Olsson & Harbison, 1953: 278, pl. 47, fig. 7.

Distribution:

Pliocene: Florida (fide Olsson & Harbison, 1953)
Pleist.:   Florida (Caloosahatchee Formation)
Recent: West Florida to Yucatan, Mexico; northern Caribbean: St. Thomas; Bahamas (museum records)

Description:

Shell: thin to moderately thick; convexity: 1.44 (fossil: 1.26); dorsal arch peaked; obliqueness: 10° (fossil: 9°); ovate; L/W: 1.36 (fossil: 1.39) (n = 30, including fossils). *Beak:* pointed, small, turned about 90° to the right, not appressed to shell margin but level with it; not excavated; does not extend far beyond the aperture. *Septum:* planar to concave, extended forward on the left side; occupying less than ½ the aperture; margin straight or with a slight median notch; edges of septum are extended forward to form ridges on the sides of the shell. *Muscle scar:* large, ovate to round; situated almost entirely in front of the septum on the right side. *Sculpture:* fine growth lines only. *Shell color:* white with reddish-brown dots merging into rays or streaks, running axially. *Life history:* unknown. *Habitat:* subtidal. *L. max.:* 38 mm; over 200 specimens, 25 localities, fossil and Recent (no significant difference in length or L/W.

Remarks:

This species is similar to *C. fornicata* in general shape, but never becomes as large, has a muscle scar, does not form large stacks, and tends to have less dense pigmentation. It has been missed as a fossil by some who have not noted the muscle scar. It is similar in septum configuration to *C. excavata,* but is smaller and flatter.

Crepidula marginalis (Broderip)   Fig. 15

Calyptraea marginalis Broderip, 1834: 38; 1835: 205, pl. 29, fig. 9 (Muerte Island and Panama). Syntypes: BM(NH) 1966630.

Distribution:

Recent: N. Chile to Panama, on both sides

of Panama Canal, and N. to Mazatlan, Mexico. Possibly in Puerto Rico (museum record).

Description:

Shell: thin, low convex (= 1.18), spatulate or triangular in shape; obliqueness: 4°; L/W: 1.20. Periostracum thin (n = 50). *Beak:* blunt, turned slightly to the right, at the level of the aperture, not rostrate or excavated. *Septum:* very shallow, planar, thin, covers ½ of aperture; sinuate margin, notched at center and at left side; growth lines and median ridge clearly visible. *Muscle scar:* absent. *Sculpture:* only growth lines (not obvious). *Shell color:* interior brown to purple; septum white to bluish; exterior tan to purple-brown with fine radiating lines, especially dense at the apex. *Life history:* unknown; adults often found inter- and subtidally on mussels. *L. max.:* 32 mm; over 200 specimens, 10 localities.

Remarks:

This species has long been confused with *C. onyx* (e.g., Parodiz, 1939), and has caused errors in the range of that species. *C. marginalis* is distinctively shaped and is never as large or as convex as *C. onyx.* It does not form stacks. It sometimes is a fouling organism on hard substrates, including wood. Its distribution on both sides of the Panama Canal could be man-mediated, but may be a result of Miocene contact between the oceans.

Crepidula monoxyla (Lesson)   Fig. 14

Calyptraea monoxyla Lesson, 1830: 391 (Bay of Islands, New Zealand). Type in Paris Museum.
Crepidula contorta Quoy & Gaimard, 1832-33: 418, pl. 72, figs. 15-16 (New Zealand).
Crypta profunda Hutton, 1873: 14 (New Zealand; Miocene and Pliocene).
Crepidula monoxyla (Lesson). Tryon, 1886: 128, pl. 37, figs. 35, 36.

Distribution:

Miocene and
  Pliocene: New Zealand (Suter, 1913)
Recent: New Zealand

Description:

Shell: thin to moderately thick; planar to low convex; obliqueness: 0°; periostracum thin. Convexity: *monoxyla* s.s.: 1.04; form *contorta:* 1.42. L/W: *monoxyla* s.s.: 1.50; form *contorta:* 1.78 (n = 40 for each form). *Beak:* small, pointed, nearly bilaterally symmetrical; at the level of the shell margin; not extending beyond aperture. *Septum:* thin, shallow, planar to concave, margin undulating (no sinus); covers less than ⅓ of aperture. *Muscle scar:* small, ovate, at right corner of septum and shell proper; smaller 2nd scar at left corner. *Sculpture:* fine growth lines; fine radial threads sometimes visible in early growth stages. Miocene specimens have more widely spaced threads (Finlay, 1927). *Shell color:* white. *L. max.:* 33 mm; 90 specimens, 13 localities. *Life history:* direct development; only 1 embryo per sac survives (Pilkington, 1974).

Remarks:

Suter (1913) equated *C. monoxyla* with *C. unguiformis,* but it is distinct on the basis of its 2 muscle scars. The double muscle insertions of *C. costata* and *C. monoxyla,* both from New Zealand, imply a relationship despite differences in more obvious characters.

C. monoxyla lives either inside dead shells and other protected places, where it is very thin and planar, or exposed on convex surfaces, where it becomes much thicker. The latter growth form has been called *C. contorta.* The 2 forms have identical muscle scars, beaks, and septal configurations. *C. profunda* is a fossil representative. *C. monoxyla* is convergent with *C. unguiformis,* as is *C. immersa,* since they differ in conservative characters (septum shape and muscle scars) while being alike in flexible features (color, convexity, and substrate preference).

Crepidula naticarum Williamson   Fig. 18

C. rugosa naticarum Williamson, 1905: 50 (San Pedro Bay, California). Types: LACM 1026.

C. coei Berry, 1950: 36 (Sunset Beach, Orange County, California). Holotype in Stanford Paleo. Type Coll. [syn. nov.] .

Distribution:

Pleist.: San Quintin, Baja California to Santa Monica, California
Recent: San Cristobal Bay, Baja California to San Pedro, California; Costa Rica (1 museum specimen) and Guatemala

Description:

Shell: thin; convexity: 1.50; obliqueness: 13°; L/W: 1.73 (n = 20). Periostracum as in *C. norrisiarum.* Aperture contracted, ovate. *Beak:* turned to the right, but nearly bilaterally symmetrical; blunted slightly, curved downward toward shell margin but slightly above it; sometimes excavated. *Septum:* moderately inserted, thin, planar; margin nearly straight with no notches, sides extended only slightly; covers ⅓ or less of aperture. *Muscle scar:* 1 anterior to right corner of septum, faint. A 2nd sometimes visible at left corner. *Sculpture:* only growth lines. *Shell color:* Beak tan or pink; rest of shell exterior light tan with fine brown lines radiating from apex; inside pink to white. *Life history:* small eggs in numerous (more than 30) egg sacs per brood; assumed to develop pelagically (personal observation on preserved specimens in LACM). *L. max.:* 31 mm; 65 specimens, 7 localities.

Remarks:

This uncommon species is superficially like *C. norrisiarum,* with which it is sympatric. Of Williamson's syntypes of *C. naticarum,* 1 specimen is *C. norrisiarum* and the other is the valid *C. naticarum. C. coei* is a straightforward synonym.

Crepidula norrisiarum Williamson   Fig. 17

C. rugosa norrisiarum Williamson, 1905: 50 (San Pedro Bay, California). Syntypes: LACM 1027.

Distribution:

Pliocene: San Diego, California
Pleist.: Los Angeles, California
Recent: Boca de la Playa, Baja California to Point Reyes, California

Description:

Shell: moderately thick; convexity: 1.31; obliqueness: 6°; L/W: 1.40; shiny, thin periostracum; aperture ovate, expanded at the point of contact with the substrate (n = 30). *Beak:* untwisted, nearly bilaterally symmetrical, rostrate, curved downward toward the shell margin but free of it (at the margin or slightly above it); usually excavated. *Septum:* deeply inserted, planar or concave; ridged along the midline; margin broadly U-shaped with a small central notch in young shells; sides extend forward; covers just less than ½ the aperture. *Muscle scar:* 2 scars, 1 anterior to each corner of septum; ovate, equal in size; very distinct. *Sculpture:* only growth lines. *Shell color:* beak region pink; rest of shell exterior light reddish-brown with fine brown radiating lines; inside pink to tan; septum white. *Life history:* large eggs 0.50 mm in diameter; no planktonic larval stage (Coe, 1949). *L. max.:* 35 mm; 40 specimens, 6 localities.

Remarks:

This species is usually on small stones or shells, living offshore in 6-20 m of water (MacGinitie & MacGinitie, 1964). Rarely, it is intertidal. It has been confused with the form of *C. onyx* growing on ribbed bivalves. The ecologically equivalent species in the Western Atlantic is *C. maculosa. C. norrisiarum* differs from *C. adunca* in color pattern and septal shape, and is consistently more elongate and slightly larger.

Pliocene fossils reported as *C. excavata* (Broderip) by Woodring et al. (1946) match the description of *C. norrisiarum* much more closely. Unworked fossils in the collections at the San Diego Natural History Museum from the San Diego Formation also appear to be this species. Many Recent *C. norrisiarum* shells have been misidentified as *C. excavata,* or as *C. arenata* (Broderip), although the 2 muscle scars, smaller size, and shape of the septum of *C. norrisiarum* make it quite distinct.

Crepidula onyx Sowerby　　　　　　Fig. 16

C. onyx Sowerby, 1824: fig. 2, descriptive letterpress (no locality).
Calyptraea amygdalus Valenciennes, 1846: pl. 15, fig. 3 (no locality).
C. rugosa "Nuttall" Carpenter, 1856: 224, ex Jay, 1839: 41 (Upper California). Nomen nudum. Possible syntypes: BM(NH). Non *C. rugosa* Anton, 1839.

C. onyx Sowerby. Carpenter, 1857a: 278.
C. onyx Sowerby. Dall, 1909b: 174, pl. 23, figs. 2, 5.
C. onyx Sowerby. Parodiz, 1939: 700, pl. 1, fig. 1.

Distribution:

Miocene: Southern California
Pliocene: San Diego to Los Angeles County, California
Pleist.: Baja California to Palos Verdes, California (Woodring et al., 1946)
Recent: Puntarenas, Costa Rica to San Pedro, California; possibly as far S as Panama (Pacific only)

Description:

Shell: thick; convexity: 1.41; obliqueness: 12°; ovate; L/W: 1.55; covered with shaggy brown periostracum (n = 50). *Beak:* blunt; turned 90° to the right; at level of aperture; not rostrate; not excavated; not extending beyond aperture. *Septum:* shallow, thick, opaque, concave; covers ½ or more of aperture; margin with a notch at left side and in center. *Muscle scar:* absent. *Sculpture:* only growth lines, often coarse. *Shell color:* inside: chocolate brown, white septum ringed with brown; outside: brown to tan, intergrading; dark radial lines. *Life history:* numerous small eggs 0.16-0.18 mm in diameter; planktonic larval stage; adults form large stacks. *Radula* (Fig. 24): inner marginal: $\frac{5}{2}$ to $\frac{8}{4}$. Outer marginal: $\frac{2}{0}$ to $\frac{4}{0}$. Other formulae below. *L. max.:* 67 mm; over 200 specimens, 15 localities.

Remarks:

This species is, in shape, size, and habits, the ecological equivalent of *Crepidula fornicata* of the Western Atlantic. Its distribution is more southern and it has not been as successful in invading new regions.

The synonym *C. rugosa* "Nuttall" Carpenter is based on a form which grew on a ribbed shell. *C. aplysioides* Reeve from Brasil and Argentina is flattened and lighter in color, with a narrow beak and a rounded aperture. It is not *C. onyx,* as thought by Parodiz (1939). Comparison of details of the radula of *C. onyx* with the Argentinian material illustrated by Parodiz confirms the distinction. The central tooth of *C. onyx* is

proportionally broader and has a formula of between $\frac{4\text{-}1\text{-}3}{0\text{-}0}$ and $\frac{2\text{-}1\text{-}2}{0\text{-}0}$. Parodiz's drawing shows a formula of $\frac{0\text{-}1\text{-}0}{0\text{-}0}$. Parodiz's lateral is hook-shaped with no cusps, while in *C. onyx* it is a complicated tooth with a formula of $\frac{2\text{-}1\text{-}5}{0}$ to $\frac{3\text{-}1\text{-}6}{0}$.

Parodiz (1939) considers *C. marginalis* a synonym of *C. onyx,* and from Broderip's original illustration I might agree. However, study of intrapopulation variability proves the distinctness of *C. marginalis* in septal shape and convexity.

Parodiz (1939) synonymizes *C. porcellana* (Linnaeus) from West Africa under *C. onyx.* Not only are there morphological differences, but Knudsen (1950) states that *C. porcellana* has eggs 0.5 mm in diameter, and releases the young at the crawling stage; hence it is unlike *C. onyx* in this respect. Dall (1909b) erroneously places *C. hepatica* Deshayes (unknown locality) under *C. onyx;* it has a similar liver shell color but is always smaller, narrower, and more rostrate. Olsson & Harbison (1953) add confusion in stating that "*C. onyx* Sowerby from the Pacific Coast of Central America" has a muscle scar. The specimens to which they refer were misidentified.

C. onyx is variable in shape, thickness, color, and size along the length of its geographic range. Some specimens from Baja California are small and pale in color. Anatomically, *C. onyx* differs from *C. fornicata* (and all other *Crepidula* species I have seen alive) in having a mantle margin pigmented with dark radial stripes and fringed with short tentacle-like extensions. Also, the penis does not always resorb in the female stage. This is true in *C. convexa* as well, but not in *C. fornicata.* The veliger of *C. onyx* differs from that of *C. fornicata* in having proportionally longer cilia on the velum and more intense pigment spots.

Crepidula pileum (Gabb)

> *Crypta (Spirocrypta) pileum* Gabb, 1864: 137, 228, pl. 29, figs. 233a,b (Tejon, California; Eocene).
> *Crepidula pileum* (Gabb). Dall, 1892: 358.
> Unnamed *Crepidula* "precursor," sp. nov., Dall, 1910: 119, pl. 9, fig. 3 (Chichagof Cove, Alaska; upper beds,

Eocene).
> *C. inornata* Dickerson, 1916: 432, 489, pl. 38, figs. 5a,b (Tejon, California; Eocene).
> *C. dickersoni* Weaver & Palmer, 1922: 31, pl. 11, fig. 2; pl. 12, fig. 9 (West bank of Cowlitz River, Lewis County, Washington). Type in University of Washington Paleo. Coll. [fide Stewart, 1926: 342].

Distribution:

Upper Eocene: California (Tejon Group); Washington State; ?Alaska (dating uncertain)

Description (from original description):

> *Shell:* globose; L/W: 1.30. *Beak:* small; 1 whorl at least, turned and appressed to side of shell; not rostrate; not excavated. *Septum:* shallow, concave, oblique; margin sinuous; covers ⅓ of aperture. *Muscle scar:* unknown. *Sculpture:* only fine growth lines. *L. max.:* 15.5 mm.

Remarks:

The importance of *C. pileum* is that it dates the genus *Crepidula* in the Eocene of California. Another calyptraeid, *Galeropsis excentricus* (Gabb), was found at the same locality (Conrad, 1866). Dall (1910: 119) describes a *Crepidula* "precursor" from the Eocene of Alaska (Chichagof Cove) of the same size and general shape as *C. pileum.* According to Dall, the primary difference is a "beak less spiral" in the new unnamed specimen. This is not a species-discriminating character. The septum of Dall's "species" is inaccessible.

Crepidula plana: see *C. unguiformis* group.

Crepidula princeps Conrad

> *C. princeps* Conrad, 1856: 326, pl. 6, figs. 52-52a (Santa Barbara, Santa Barbara Formation; Late Pliocene-Early Pleistocene). Holotype: USNM 1839.
> *C. princeps* Conrad. Addicott, 1970: 63, pl. 4, figs. 16, 19-21.

Distribution:

Miocene: San Diego to southern Washington State

Pliocene: San Diego to Washington State
(including Empire Formation, Oregon)

Pleist.:   Santa Barbara to Monterey, California (rare, adventitious?)

Crepidula princeps var. praerupta Conrad

C. *praerupta* Conrad, 1849: append., p. 727, pl. 19, figs. 9-10 (Astoria, Oregon; Miocene). Lectotype: USNM 3564.

C. *ungana* Dall, 1910: 119, pl. 10, figs. 8-9 (Coal Bluff, Unger Island, Alaska; Miocene). Holotype: USNM.

Distribution:

?Eocene: Oregon (Conrad, 1866; dating may be in error)
Oligo.:   Washington State
Miocene: Oregon (Astoria Formation); Alaska (Dall, 1892); Upper Vaqueros (L. Miocene) of California (Loel & Corey, 1932); Templar Formation (U. Miocene) of Bakersfield, California

Description:

Shell: massive, highly convex; oblique; aperture elliptical; L/W: 1.50; largest known species (n = 50). *Beak:* large, sharply twisted to right side and turned upward, often appressed to body whorl above plane of aperture; not rostrate; not excavated; early whorl inflated, extending behind and lateral to the aperture; a sulcus between beak (1st whorl) and major body whorl. *Septum:* recessed, thick, concave; attached farther forward on left side; margin curved with wide notch at right side; covers ½ of aperture. *Muscle scar:* large, ovate to round, forward of shelf on right side of shell. *Sculpture:* none except fine growth lines.

Life history: lived in stacks and clumps in muddy bays, occurring in high density in some areas; often bored by sponges and *Polinices* sp. *L. max.:* 125 mm; over 200 specimens, 18 localities.

Remarks:

The specimens named *C. praerupta* differ from *C. princeps* by being shorter (max. length: 30 mm) and less massive. According to Moore (1963: 26) they differ also in that "the apex is curved in a plane that parallels the aperture," but beak curvature varies on specimens supposed to be *C. praerupta*. The lectotype is indistinguishable from small *C. princeps,* except for a relatively narrower beak. Moore (1963) synonymizes *C. rostralis* Conrad (= *C. adunca*) with *C. praerupta* despite the rostrate, barely twisted beak of the former. *C. ungana* of the Miocene of Alaska is a specimen intermediate between *C. praerupta* and *C. princeps* (L. = 38 mm). The beak is narrow and recurved, and stacks have been preserved. Addicott (1970) points out that characters dealing with shape of the septum cannot be used to distinguish the 2 "species," nor can beak shape, nor shell convexity. Since typically large *C. princeps* have not been found co-occurring with the variant *praerupta,* the latter may well be a small subspecies of *C. princeps.*

Dall (1909a) suggests that *Crepidula princeps* found in Pleistocene strata are adventitious, derived from older adjacent faunas. However, Miocene specimens from the Jewett Sand and Pliocene specimens from the Empire Formation (Oregon) are more coiled than early Pleistocene representatives from the Santa Barbara Formation (Addicott, 1970).

Crepidula protea d'Orbigny   Fig. 19

C. *protea* d'Orbigny, 1841: 465; 1842-53: 192, pl. 24, figs. 30-33

FIG. 20. *C. plana* from Massachusetts, 2 views; a) dorsal, L = 41.0 mm; small males occupied the shell, one is still in place; b) ventral, same specimen.

FIG. 21. *C. nummaria* from Puget Sound, 2 views; a) dorsal, L = 33.8 mm; heavy periostracum is present; b) ventral, same specimen.

FIG. 22. *C. lessonii* from Panama (Pacific), 3 views; a) dorsal, L = 19.8 mm; b) ventral, same specimen; c) lateral, showing foliations; same specimen.

FIG. 23. *C. grandis* from Bering Strait, Alaska, 3 views; a) dorsal, with flaking periostracum; L = 56.3 mm; b) ventral, same specimen; muscle scar is accentuated with ink lines; c) lateral, same specimen.
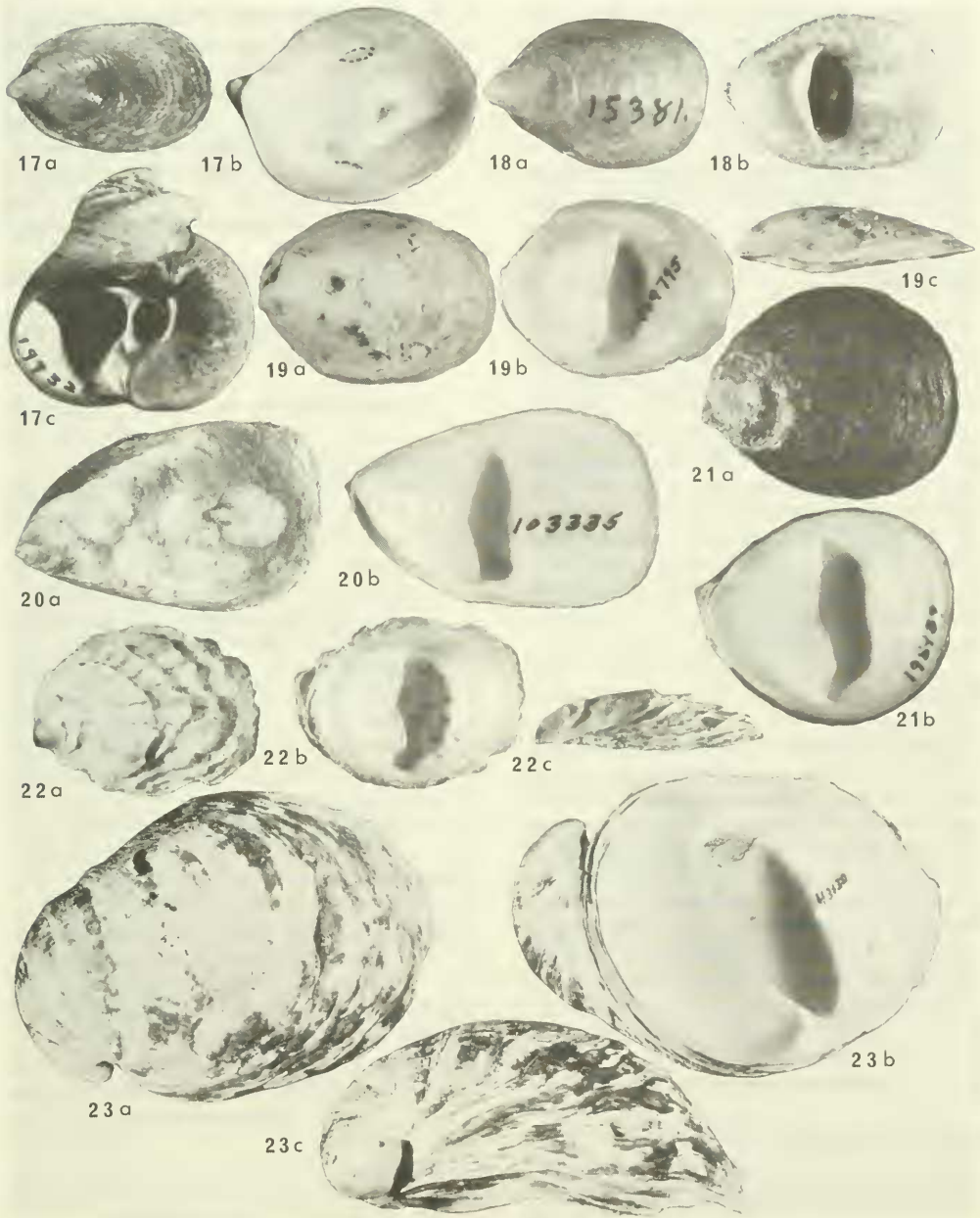
FIG. 17. *Crepidula norrisiarum* from Southern California, 3 views; a) dorsal, L = 18.6 mm; b) ventral, L = 32.5 mm; muscle scars were accentuated with ink dots; c) lateral, male and female on a *Norrisia* shell; L of female = 19.5 mm.

FIG. 18. Paratype of *C. coei* Berry (= *C. naticarum*) from Southern California, 2 views; a) dorsal, L = 14.6 mm; b) ventral, same specimen.

FIG. 19. *C. protea* from Brazil, 3 views; a) dorsal, L = 30.8 mm; b) ventral, same specimen; c) lateral, same specimen.

(Antilles; coast of Patagonia; "Maldonado, Brazil").

C. protea d'Orbigny. Parodiz, 1939: 702.

Distribution:

Pliocene: Argentina
Pleist.:   Argentina
Recent: Atlantic coast of South America, southernmost Antilles to Patagonia

Description:

Shell: thin, planar to slightly convex, convexity: 1.19; obliqueness: 5°; aperture subcircular; L/W: 1.30; thick periostracum (n = 12). *Beak:* small, turned slightly to right, at level of or above shell margin; does not extend beyond it; not excavated. *Septum:* shallow, planar; sulcus at left side, slight notch in center of margin; covers slightly less than ½ aperture. *Muscle scar:* absent. *Sculpture:* none except growth lines. *Shell color:* white to tan; often yellow lines along sides of septum. *L. max.:* 33 mm; 12 specimens, 3 localities.

Remarks:

Crepidula protea occupies flat, dark, sheltered sites. From its septal configuration it appears to be closely related to *C. dilatata,* but lack of a muscle scar suggests a close relationship with *C. unguiformis.* It may be an offshoot from the *C. unguiformis-plana* group. D'Orbigny states vaguely that North American specimens (*C. plana,* undoubtedly) might be within his concept of *C. protea.* Dall (1889c) suggests that *C. protea* equals *C. unguiformis.*

Crepidula unguiformis group

Crepidula unguiformis Lamarck

Patella crepidula Linnaeus, 1767: 1257 (Mediterranean Sea). Type: Linnaean Society, London, no. 587. Nomen oblitum.
?*P. goreensis* Gmelin, 1791: 3694 (Isle Gorée [West Senegal]).
Crepidula fasciata de Roissy, 1805: 238 (Senegal and the Mediterranean Sea). Nomen oblitum.
C. italica Defrance, 1818: 397 (no local-ity; Tertiary). Nomen oblitum.
C. unguiformis Lamarck, 1822: 25 (Barbary [Northern Africa]). Type in Geneva Museum, fide Mermod, 1950: 723.
C. sinuosa Turton, 1825: 364, pl. 13, fig. 5 (Scarborough, Yorkshire, England) [fide Philippi, 1836: 120].
C. candida Risso, 1826: 255, pl. 10, fig. 138 (Nice and the Maritime Alps, France; Tertiary) [fide Saussaye, 1869: 96].
C. crepidula (Linnaeus). O. G. Costa, 1829: 120, 125.
C. calceolina Deshayes, 1830: 26 (Indian Ocean; fossil in Italy, Sicily, and near Vienna).
C. sandaliformis de Serres, 1830: 77 (Upper deposits, eastern Pyrenees; Tertiary) [syn. nov.].
C. sandalina Deshayes, 1833: append., pl. 2-3 (Sicily, Pliocene; Bordeaux, Miocene; Europe, Recent) [syn. nov.].
C. rugosa Anton, 1839: 28 (no locality, fossil).
C. unguiformis Lamarck. C. B. Adams, 1852: 230 (complete synonymy).
?*C. deshayesii* Folin, 1867: 28, pl 4, figs. 9-10; (Pearl Islands [Panama, Pacific]) [fide Tryon, 1886]. Syntypes: Museum d'Histoire Nat. de Bayonne (fide Kisch, 1960: 145).
C. unguiformis Lamarck. Bucquoy et al., 1886: 460, pl. 55, figs. 8-11.

Distribution:

Miocene: Vienna Basin; southern France; Switzerland; N. Italy; Venlo, Holland
Pliocene: Italy; Algeria; Belgium; S. France
Pleist.:   Monte Pellegrino (Italy)
Recent: Mediterranean and Adriatic Seas; coast of Portugal; ?West Africa (all from museum and literature records)

Description:

Shell: thickness variable; convexity: -1.08; obliqueness: 3°; aperture ovate to spatulate; L/W: 1.43 (n = 20). *Beak:* pointed, directed posteriorly; at level of shell margin but detached from it; protoconch minute. *Septum:* shallow, often convex; sulcus at left side and shallow notch in center of septal margin; ridged along midline

in young shells; septum covers ⅓ to ½ of aperture. *Muscle scar:* absent. *Sculpture:* none except growth lines. *Shell color:* white or tinged with yellow; yellowish periostracum. *Life history:* preferred habitat inside dead shells of other gastropods or under rocks; does not form stacks of more than 3. *L. max.:* 38 mm; over 50 specimens, 19 localities, fossil and Recent combined.

Remarks: follow *C. plana.*

Crepidula unguiformis var. cochleare Baserot

C. *cochleare* Baserot, 1825: 71, pl. 5, fig. 10 (Mérignac, France; Tertiary).

Distribution:

Miocene, Pliocene: Vienna, Bordeaux, Italy

Description (differences from *C. unguiformis*):

Shell: convexity: 1.20; obliqueness: 4°; L/W: 1.44. *Beak:* nearly bilaterally symmetrical, prominent.

Remarks: follow *C. plana.*

Crepidula plana Say   Fig. 20

C. *plana* Say, July, 1822: 226 (coast of the United States). Type lost.
C. *depressa* Say, 1822: 225 (southern coast of the United States). Type lost.
C. *lamina* H. C. Lea, 1843: 164. Nomen nudum; 1846: 250, pl. 35, fig. 42 (Petersburg, Virginia; Tertiary).
C. *rhyssema* Olsson & Harbison, 1953: 278, pl. 47, figs. 4, 4a-c (St. Petersburg, Florida; Pliocene) [syn. nov.]. Holotype: ANSP 18026.

Distribution:

Miocene: Santo Domingo to Nantucket, Massachusetts (including Yorktown Formation)
Pliocene: Florida to Massachusetts (including later stages of Yorktown Formation)
Pleist.: Florida to Nantucket, Massachusetts (including Waccamaw, Caloosahatchee Formations)
Recent: Trinidad to Prince Edward Island;

Buenos Aires to Uruguay; parts of Venezuela; Texas

Description (differences from *C. unguiformis*):

Shell: convexity: 1.00; obliqueness: 0°; L/W: 1.66. *Life history:* planktonic larval stage (unknown for *C. unguiformis*). Egg diameter 0.136 mm (Conklin, 1897). *Radula* (fig. 24): central tooth formula: $\frac{3\text{-}1\text{-}3}{0\text{-}0}$ to $\frac{4\text{-}1\text{-}4}{0\text{-}0}$. Lateral: $\frac{2\text{-}1\text{-}6}{0}$ to $\frac{2\text{-}1\text{-}9}{0}$. Inner marginal: $\frac{7}{2}$ to $\frac{12}{5}$ (most of the variability is between radulae). Outer marginal: $\frac{3}{0}$ to $\frac{8}{0}$ (most often $\frac{5}{0}$). *L. max.:* 47 mm; over 200 specimens, over 50 localities (Recent). Fossil specimens not significantly different in size or shape.

Remarks:

The *Crepidula unguiformis* group is composed of the white, flat *Crepidula* species with photonegative habits and which are found in Europe and the Western Atlantic. As was customary at the time, Lamarck (1822) provided the name *C. unguiformis* in order to avoid tautonymy. The type-specimens of *Patella crepidula* in the Linnaean collection are actually *Crepidula walshi* of the Indian Ocean and China Sea. Because there are unusually many specimens for Linnaeus' time (6) and because the type-locality is the Mediterranean Sea, it appears that the specimens have been replaced. To clarify the matter, specimens from the Museum Ludovicae Ulricae Reginae must be examined, as the published descriptions are too vague to distinguish *C. walshi* from *C. unguiformis.*

Crepidula sinuosa, C. candida, C. calceolina and *C. sandalina* are straightforward synonyms; *C. sandaliformis* is an irregular form with deeply impressed growth lines. *Calyptraea* (= *Crepidula*) *monoxyla* (Lesson) from New Zealand was thought by Suter (1913) to be *C. unguiformis,* but is distinct. Some specimens of *C. monoxyla* are labeled *C. crepidula* in American collections (MCZ; ANSP). The Eastern Pacific locality and the description indicate that *C. deshayesii* could equal *C. lessonii* (Ranson, in Kisch, 1960).

C. goreensis from the island of Gorée may be a foliated form of *C. unguiformis.*

Crepidula cochleare is slightly convex, and is probably only a form of *C. unguiformis* occupying a convex substrate. There are also Florida Miocene specimens with this shell shape, and comparable specimens can be found in the Mediterranean Sea today.

Indistinguishable from *Crepidula unguiformis* on the basis of shell characters is *C. plana* of the Western Atlantic. Several authors have pointed out the seeming identity (C. B. Adams, 1852; Bucquoy et al., 1886), but have been reluctant to synonymize them due to geographical distinctions. Both names are well-established in the literature. The cryptic, clinging habit of this snail (attachment to wood, man-made substrate and loose objects such as dead shells often co-occupied by hermit crabs) coupled with its 2-to-5 week planktonic larval stage, makes it possible for the same species to be distributed on both sides of the Atlantic. Both *C. plana* and *C. unguiformis* are eurytopic. Some specimens of *C. unguiformis* from Greece have brown pigment on the shell, but a few from Texas do also.

The name *Crepidula depressa* Say has page precedence over *C. plana,* but never came into use. *C. lamina* was described from weathered fossil material with prominent growth lines. *C. rhyssema* is also fossil, a slightly convex form.

Some members of the Pacific species group to be described next have been called *Crepidula unguiformis.* This would give the species broad longitudinal distribution in nearly all latitudes. This is a rare situation among shallow-water gastropods including *Crepidula,* and is contra-indicated by consistent differences in color (*C. lessonii, C. striolata*) and larval form (*C. nummaria, C. perforans*).

Gray (1857) figured the radula of the European *Crepidula unguiformis.* Comparison with the radulae of several individuals of *C. plana* and a drawing in Dall (1889b) of a *C. plana* radula reveal no consistent differences (Fig. 24). The inner marginal tends to have fewer cusps in *C. plana* than shown in Gray's drawing, but the number is variable, and Gray's figure appears to be slightly stylized. The outer marginal of *C. plana* has 5 small cusps not shown by Gray, but occasionally they are absent. Thus *C. plana* and *C. unguiformis* could be synonymous on the basis of radula characters. If they are the

same species, *C. plana* and *C. unguiformis* have disjunct distributions (separated by the Atlantic Ocean) with low gene flow. Final disposition of the matter awaits anatomical study of *C. unguiformis.*

The veligers of *Crepidula plana* and *C. fornicata* are readily distinguished by a near total lack of pigment spots in the former. Settling veligers of *C. plana* are photonegative whereas those of *C. fornicata* are photopositive.

Eastern Pacific planar **Crepidula** group

Crepidula nummaria Gould   Fig. 21

> *C. nummaria* Gould, 1846: 160 (Classet, Puget Sound [Washington]). Holotype: USNM 5870.
>
> ?*C. minuta* Middendorff, 1849a: 101, pl. 11, figs. 6-7 (Sitcha Island, Alaska) [syn. nov.].
>
> *C. navicelloides* "Nuttall" Carpenter, 1864 (ex Jay, 1839: 41): 654 (Upper California). Nomen nudum.
>
> *Crypta (Ianacus) unguiculus* H. & A. Adams, 1858 (ex Sowerby ms.): 370 (no locality) [syn. nov.] .
>
> *Crepidula nivea* var. *glottidiarum* Dall, 1905: 26 (San Pedro, California).

Distribution:

Pliocene: San Diego to Monterey, California (Grant & Gale, 1931)

Pleist.:   San Pedro to Monterey, California

Recent: San Pedro to Puget Sound (LACM); Mount Edgecumbe, Alaska (Dehnel, 1955); Mazatlan to Bering Strait (Dall, 1921)

Description:

Shell: thick; convexity: 1.10; obliqueness: 1°; L/W: 1.38 (variable); shaggy, brown periostracum (n = 50). *Beak:* small, straight or inclined slightly to right; at level of shell margin; not excavated; beak does not extend beyond aperture. *Septum:* shallow, planar to convex, ridged along midline; covers less than ½ aperture; moderately deep, U-shaped sulcus at left side and shallow notch to right of or at center of septal margin. *Muscle scar:* absent. *Sculpture:* only growth lines. *Color:* white. *Life history:* no planktonic larval stage; early embryo diame-

ter: 0.40 mm (Dehnel, 1955). *L. max.:* 40 mm; over 200 specimens, over 50 localities.

Remarks: follow *C. striolata.*

Crepidula lessonii (Broderip) Fig. 22

> *Calyptraea lessonii* Broderip, 1834: 39; 1835: 204, pl. 29, fig. 5 (Island of Muerte [Ecuador]).

Distribution:

Recent: Paita, Peru, to San Felipe, Baja California

Description:

Shell: thick, laminated; concave to slightly convex; convexity:1.07; obliqueness: 0.3° subcircular to ovate; L/W: 1.28 (n = 15). *Beak:* curved to right side; at or slightly above level of aperture, not extending beyond it; not excavated. *Septum:* as in *C. nummaria*; deep sulcus at left side. *Muscle scar:* absent. *Sculpture:* growth lines prominent; laminated. *Shell color:* white, often streaked with brown rays; white interior, sometimes with brown spots or rays; apex with pigment in most cases. *Life History:* found under rocks; larval stage unknown. *L. max.:* 28 mm; 50 specimens, 10 localities.

Remarks: follow *C. striolata.*

Crepidula perforans Valenciennes

> *C. perforans* Valenciennes, 1846: pl. 24, fig. 9 (Pacific America).
> *C. explanata* Gould, 1853: 377, pl. 14, fig. 7 (Monterey and Lower California). Holotype: MCZ 169137; paratypes: MCZ 169138.
> *C. fimbriata* Reeve, 1859: pl. 2, fig. 11 (Vancouver Straits, Canada).
> *C. exuviata* "Nuttall" Reeve, 1859 (ex Jay, 1839: 41): pl. 5, fig. 28 (Monterey, California).

Distribution:

Pleist.: Monterey, California
Recent: Mazatlan to Monterey, California; to Vancouver Straits, Canada (distribution patchy)

Description:

Shell: thickness variable; shell layers often separated; concavity: −1.05; obliqueness: 0.3°; elongate; L/W: 1.79 (n = 25); periostracum thin. *Beak:* large larval shell, beak directed almost posteriorly; at level of aperture, not extending beyond it; not excavated. *Septum:* as in *C. nummaria. Muscle scar:* absent. *Sculpture:* growth lines prominent; often, when in pholad hole, a groove runs from anterior to posterior on the dorsal surface, forming a water channel. *Shell color:* white. *Life history:* nonplanktonic development. Egg diameter: 0.5 mm (Coe, 1949). *L. max.:* 35 mm; 50 specimens, 5 localities.

Remarks: follow *C. striolata.*

Crepidula nivea C. B. Adams

> *C. nivea* C. B. Adams, 1852: 234 (Panama). Lectotype: MCZ 186291; paralectotype: MCZ 186292.
> *C. nebulata* Mabille, 1895: 57 (Lower California). Type in Paris Museum.

Distribution:

Recent: Panama to Southern California

Description (differences from *C. nummaria*):

Shell: thin; periostracum moderately developed. *Beak:* protoconch tiny. *Sculpture:* apical riblets. *Shell color:* entirely white (unlike *C. striolata*). *L. max.:* 45 mm; 35 specimens, 5 localities.

Remarks: follow *C. striolata.*

Crepidula striolata Menke

> *Calyptraea squama* Broderip, 1834: 40; 1835: 205, pl. 29, fig. 10 (Panama). Non *Calyptraea squama* Deshayes, 1830.
> *Crepidula striolata* Menke, 1851: 35 (Mazatlan, Mexico).
> *C. strigellata* Dunker, 1853: 111 (no locality). Syntypes in BM(NH). [syn. nov.]
> *C. williamsi* Coe, 1947: 241, text figs. (at 16 meters off North Coronado Island, Lower California). Holotype: Calif. Acad. Sci.; paratypes: San Diego NHM [syn. nov.].

Distribution:

Recent: Canal Zone, Panama to San Diego,
California

Description (differences from *C. lessonii*):

Shell: thinner. *Sculpture:* growth lines
only. *Shell color:* white with brown rays at
apex, rarely extending the full length of the
shell. *Life history:* broods young; no plank-
tonic larval stage. Egg diameter: 0.45 mm
(Coe, 1949); often in tidepools. *L. max.:*
35 mm; 30 specimens, 4 localities.

Remarks for the entire Eastern Pacific
planar *Crepidula* group:

This is the most difficult species group to
deal with on the basis of shell characters.
The fossils, with the exception of foliated
individuals from Monterey, look alike
throughout the Eastern Pacific coastal re-
gion. Carpenter (1957a) wrote that the
various growth forms of white Pacific
Crepidula should all be referred to *C. nivea*
on the basis of shell characters; the degree of
foliation, coloring, and septal shape are
variable within the named forms.

These Pacific forms often have a promi-
nent, slightly turned apex and a deep septal
notch, as well as some pigmentation, which
separate them from the *C. unguiformis-C.
plana* group. They are more variable in
habitat as well, for the Atlantic species is not
common underneath boulders as is *C. num-
maria,* but prefers the smooth inner surfaces
of shells. *C. nummaria* is a shallow-water
species and is found in tidepools. The Pacific
and Atlantic planar *Crepidula* species must
have been long isolated, but within the last
50 years oyster transplantation has brought
C. plana potentially in contact with the
native Pacific snails. However, J. Carlton
(personal communication) states that *C.
plana* remains inside bay regions, while *C.
nummaria* and *C. perforans* are outside.

On the basis of shell characters, it is not
possible to tell if the Eastern Pacific and
Western Atlantic groups have diverged or if
their origins were separate. The two groups
share such stable traits as muscle placement
and septal shape. They possibly evolved
from a common stock in the Miocene, when
the oceans communicated in the region of
Panama. The Pacific *C. perforans,* as I have
defined it, is morphologically similar to *C.

unguiformis, and in fact Carpenter (1857a;
1863) used the name *C. unguiformis* for the
Pacific species.

C. lessonii is separable from the other
basically Pacific white *Crepidula* species by
its unique color pattern, high degree of
lamination, deep septal sulcus, and smaller
adult size. *C. striolata* is smooth; often the
pigment occurs only at the apex. There are
ecological differences between the 2 forms,
due to life in different microhabitats. *C.
lessonii* was described from specimens occur-
ring under large rocks, in protected regions.
Specimens of *C. lessonii* are laminated in
varying degrees, that is, the shell layers are
separated at the growth lines. Lamination is
enhanced by life in still waters; it occurs
most obviously in thick shells such as those
depositing extra calcium carbonate to com-
bat boring sponges. There seems to be a
genetic component in the capacity to form
laminations, with degree of expression of the
trait depending on local conditions. Lamin-
ated shells are not found in the *C. ungui-
formis* group in similar habitats. There are
specimens intermediate in degree of shell
lamination, hence *C. striolata* might equal *C.
lessonii.* One population from Panama
(ANSP 154029 and 154031) shows a range
of variation, and is difficult to sort into *C.
striolata* and *C. lessonii.* Carpenter (1857b,
pl. 8) shows the range of growth forms of
both *C. lessonii* and *C. nummaria.*

Smith (1946) separates *C. perforans* and
C. nivea on admittedly weak evidence of
shell shape and species ranges. *C. perforans* is
widespread, and can occupy abandoned
pholad holes. But more than 1 white species
can use this substrate; taxonomy should not
be based on it. The shell thickness of *C.
perforans* is highly variable depending upon
the substrate. Specimens from pholad holes
are thick; those living on other shells are
thin.

Smith (1946) separates *C. nivea* and *C.
nummaria* on the strength of periostracum
development. I have found intermediates,
and dispute the usefulness of this character
alone. Carpenter (1863) stresses the small
riblets on the apex of *C. nivea,* but these
disappear on worn shells, including most
adults. *C. nivea* does have a smaller proto-
conch than *C. nummaria* (Berry, 1955), but
this character can only be observed on
young, well-preserved shells. Keen (1971)
synonymized *C. nivea* under *C. striolata.*

Dehnel (1955) studied growth of 1 planar

Crepidula species from Southern California and Mount Edgecumbe, Alaska. He called the species *C. nummaria* but did not figure or describe the adult, nor did he mention taxonomic difficulties. The animal brooded its young to the crawling stage, with 20-600 young per brood.

Illustrated specimens of the Alaskan *Crepidula minuta* are small and planar. It would be of interest to examine their method of rearing young; presence of a planktonic larval stage would separate them from *C. nummaria. C. nivea* var. *glottidiarum* is a form living on the brachiopod *Glottidia*; some individuals so identified are *C. naticarum. C. depressa* Lesson (1830: 394) from Chile and Peru is also a synonym of one of the Pacific white planar *Crepidula* species, but which one cannot be established.

The arrangement of species above is tentative, making the best sense out of insufficient data and historical errors. It might possibly be that brooding of the young is a trait varying intraspecifically in some species. This is known to be true for the polychaete *Cirriformis tentaculata* (George, 1967) and has been reported in 3 species of vermetids (Hadfield, 1972), which may facultatively retain embryos. However, brooding to the crawling stage in *Crepidula* is accompanied by mandatory production of fewer, larger, yolkier eggs, and absence of a planktotrophic larval stage. *Crepidula* species with partial brooding produce planktotrophic young. Those *Crepidula* species occupying restricted habitats such as pholad holes have selection pressure for retaining the young so that they are insured favorable substrate.

Experiments testing genetic variability within this species complex would be valuable in unraveling its history and present status.

Crepidula walshi Reeve

   C. excisa Philippi, 1849: 24 (Mergui, Burma, inside empty shell). Type lost. Nomen oblitum.

   Calyptraea plana Adams & Reeve, 1850: 70, pl. 11, fig. 3 (China Sea). Non *Crepidula plana* Say, 1822.

   Crypta (Ergaea) walshi "Herrmannsen" H. & A. Adams, 1858: 370 (Singapore and Ceylon). Nomen nudum.

   C. plana (Adams & Reeve). H. & A. Adams, 1858: 370.

   Crepidula walshi [(H. & A. Adams)]. Reeve (ex "Herrmannsen"), 1859: pl. 3, figs. 17a,b (Singapore and Ceylon).

   C. scabies Reeve, 1859: pl. 3, fig. 18 (China Sea). Type in BM(NH).

   Crypta lamellosa A. Adams, 1862: 297 (Gotto Islands, Japan, 88 m).

   Ergaea walshi [(H. & A. Adams)]. Gray (ex "Herrmannsen"), 1867: 740.

   Crepidula walshi [(H. & A. Adams)]. Tryon (ex "Herrmannsen"), 1886: 130, pl. 38, figs. 56-58.

   C. orbella Yokoyama, 1920: 76, pl. 4, figs. 22-23 (Naganuma Zone, Miura Peninsula, Japan; Upper Pliocene). [syn. nov.].

Distribution:

U. Pliocene: Japan: Naganuma Zone (Yokoyama, 1920); Miura and Boso Peninsulas (Taki, 1938)

Recent: Japan; Iranian Gulf (Thorson, 1940); China Sea; Indian Ocean to Borneo. From Japan to as far S. as Arafura Sea off Darwin, Australia

Description:

Shell: small to medium sized, thin; convexity: −1.08; obliqueness: $5°$; aperture wider than long; L/W: 0.79; right side more expanded than left (n = 20). *Beak:* miniscule, twisted to right; near level of posterior margin; not excavated; expansion rate rapid. *Septum:* shallow, convex; attached along posterior margin and only ½ the length of its sides; overlapping fold in septum; septum covers about ¼ of aperture. *Muscle scar:* absent. *Sculpture:* fine growth lines. *Shell color:* entirely white. *Life history:* larval stage planktonic; egg diameter: 0.19 mm (Ishiki, 1939). *L. max.:* 26 mm; 50 specimens, 8 localities. *W. max.:* 30 mm; 65 specimens, 14 localities.

Remarks:

Once placed in the subgenus *Siphopatella* Lesson, *Crepidula walshi* is closest to the genus *Crucibulum* of all the species of *Crepidula*. Several other generic names have been erected for it (Taki, 1933, 1938; Table 4). Its geographical distribution in the Near and Far East is unique in *Crepidula. C. scabies* is probably an irregular growth form,

as is *C. orbella. C. lamellosa* is a laminated form. *C. chinensis* Gray may be a synonym (see *nomina dubia* section).

Crepidula wilckensi Finlay

> *C. incurva* Zittel, in Zittel et al., 1864: 44, pl. 15, fig. 9 (New Zealand; Tertiary). Non *C. incurva* Broderip, 1834.
> *C. wilckensi* Finlay, 1924: 101. New name for *C. incurva* Zittel, 1864, non *C. incurva* Broderip, 1834.

Distribution: As above.

Description (after Finlay, 1924):

Shell: ovate, moderately to highly convex, similar to that of *C. gregaria. Beak:* more tapering than on *C. gregaria. Septum:* longer than in *C. gregaria*; margin concave, not bisinuate. *Muscle scar:* unreported. *Sculpture:* faint growth lines. *Shell color:* unreported.

Remarks:

According to Finlay (1924), this form is not synonymous with *C. gregaria* as previously believed (Ortmann, 1902). The shape of the septum is the most convincing difference.

Crepidula youngi (Powell)

> *Maoricrypta youngi* Powell, 1940: 232, pl. 33, figs. 12-13 (Cape Maria van Diemen, New Zealand). Holotype: Auckland Museum; paratypes: ANSP 240358.

Distribution: As above.

Description:

Shell: ovate, low convex, moderate-sized. *Beak:* narrow, rostrate, directed posteriorly; not extending beyond aperture; not excavated. *Septum:* planar, no deep sulci, margin concave, sides produced; covers about ½ the aperture. *Muscle scar:* a weak scar at either corner of septum. *Sculpture:* faint growth lines and radial costae; regularly-spaced pits. *Shell color:* tan with brown streaks. *L.:* 27 mm (holotype).

Remarks:

The shell is very similar to *Crepidula norrisiarum* except for the sculpture pattern which is unique to *C. youngi*. This species was described from dead material, and the paratypes are badly eroded. It is probably an offshore form. Nothing is known of its ecology. I transfer it to *Crepidula* for I do not consider *Maoricrypta* valid (see discussion).

INVALID SPECIES

Crepidula juliella Weisbord, 1962: 213, pl. 19, figs. 14, 15 (Venezuela; Pleistocene).

This name is based on 2 specimen fragments, possibly juveniles, from their thinness. They do not differ in any striking feature from the larger specimens of *Crepidula* found at the same locality (*Crepidula cymbaeformis*).

Crepidula osculans C. B. Adams, 1852: 234 (Panama; Recent). Lectotype: MCZ 156277.

This, according to Carpenter (1863: 361), is really *Scutellina navicelloides* (Carpenter, 1857). *Scutellina* Gray, 1847 was considered a subgenus of *Acmaea* by Fischer (1885: 865), but is now synonymized with *Phenacolepas* (see Keen, 1971: 361).

NOMINA DUBIA

The following species are insufficiently known for full treatment, and/or may not be valid.

Crepidula chinensis (Gray), 1867: 740 (China). I have seen only 1 specimen alleged to be *C. chinensis,* from Paetel's collection. It was *C. walshi*. But from illustrations (Tryon, 1886: pl. 39, figs. 69-71) it appears that the apex of *C. chinensis* is spiraled and more central than in *C. walshi,* and if so it might be a valid species. It is limited to the South China Sea. The type is from the Cuming collection. Gray distinguished the shell from other Calyptraeidae by the fold in the septum which forms a narrow cavity. He erected the genus *Noicia* for the species.

Crepidula cooksoniae Seeley, 1861: 291, pl. 11, fig. 18 (Upper Greensand, Cretaceous; Cambridge, England). Type in the col-

lection of the University, Cambridge. Preserved as an internal mold in lime phosphate, the snail was small and bilaterally symmetrical with the apex high above the shell margin. The septum is, however, unconvincing, casting doubt on whether the fossil is a *Crepidula*.

Crepidula hepatica Deshayes, 1830: 26. Type-locality unknown. Menke (1847) used the name for shells from Mazatlan and San Blas, which Dall (1909b) thought were *C. incurva*. C. B. Adams (1852) hesitantly followed suit in naming his Panamanian material, which is very similar to the dark morph of the Grenadan *C. aplysioides*. Krauss (see C. B. Adams, 1852: 228) used *C. hepatica* for a South African species. African material which I have seen appears to be distinct from the Panamanian species. Without knowledge of Deshayes' locality or his specimens, it is impossible to say which is the original *C. hepatica,* because the brief description could fit either the Panamanian or the South African specimens.

Ianacus isabellae Taki, 1938: 146, fig. 4 (Miyazaki, Japan), is known only from the type in Taki's private collection. Based on Taki's illustration and remarks, the shell is like *C. unguiformis,* except for 2 parallel folds on the left side of the septum (from internal view). The larval stage is unknown. Habe (personal communication) doubts the validity of the species.

Crepidula incurvata Broderip & Sowerby, 1829: 370 (Kamchatka). I found no type at the British Museum (Nat. Hist.), which would have been the logical place for it. The description mentions an ovate shell with rough, thick periostracum. The apex is incurved and marginal.

Crepidula mytiloidea Bellardi & Michelotti, 1840: 74, pl. 8, figs. 9-10 (Villavernia near Tortona, Italy; Cretaceous). The type-specimen is small (L = 1 cm) and the published illustrations are very poor in part because they are not magnified. I cannot verify that this is a *Crepidula* from the illustrations.

Crepidula sitchana Middendorff, 1849a: 100, pl. 11, figs. 3-5 (Sitchana Island, Alaska). Sowerby's (1883) illustration of *C. sitchana* and the specimens at the BM(NH) are small specimens of *C. grandis.* Specimens in Paetel's collection at the Berlin Museum are *C. nummaria* and *C. norrisiarum.* The latter does not occur in Alaska and the locality given for the specimen must

therefore be in error. The localities of Paetel's specimens are notoriously inaccurate. Whether *C. sitchana* as originally conceived by Middendorff exists awaits examination of his original specimens.

Crepidula succinea Risso, 1826: 255 (living on tritons in the Mediterranean). There is no illustration or reference to a type-specimen. The description refers to a yellow-amber, very fragile shell with concentric crenulations.

DISCUSSION

1. *Taxonomic characters*

The main problem in systematics of *Crepidula* is one of separating genetic from environmentally-induced variation; that is, of determining which traits are strongly modified by the environment, which are variable, and which are invariant for a given species. The high colonizing ability of those *Crepidula* species with pelagic larvae results in few clinal differences among populations, presumably due to high gene flow. Exceptions are expected in species without planktonic larvae, although they appear to have relatively high genetic interaction through transport on other living organisms or floating objects.

Dall (1892: 355) correctly points out that shell shape in *Crepidula* facultatively adjusts to the environment, "... the influence of selection being of comparatively small importance." *Crepidula* is more plastic than any other patelliform mollusk and is rivaled only by oyster-like bivalves. The ability to conform to the substrate and to settle on a wide range of substrate types confers strong advantage on largely sedentary filter-feeders.

Phenotypic plasticity is itself an evolved trait. It is a character present in the earliest fossil *Crepidula* species, but is less well developed in *Calyptraea* and *Crucibulum*. It is more advantageous in a rapidly changing environment than is genetic polymorphism, the alternative method of acquiring flexibility within a population, for it allows a single individual to adapt itself to changing conditions within its own lifetime. Phenotypic plasticity is also advantageous in dealing with spatially heterogeneous environments; this is more important for young males which are mobile than for the more

TABLE 3. Functional and evolutionary significance of major traits.

Trait	Functional and ecological significance	Evolutionary significance
One muscle scar	Represents insertion of the major shell muscle not on the edge of the septum (= columella) as in most coiled gastropods, but on the shell itself. Edge of the septum is easily broken if force is applied to the animal. Attachment of body to the shell itself is more secure and it provides a more limpet-like clamping action (better leverage). (*Crepidula* spp. lacking this trait have alternative ways of improving shell attachment for sedentary existence).	This is a specialization for limpet-like existence. It appears in all morpho-ecological groupings of *Crepidula*.
Two muscle scars	Represents a "split" shell muscle, inserting on both sides of the septum aiding in sustaining the animal's position on its substrate and in its shell.	This is perhaps more highly specialized than 1 muscle scar. Species showing it are all from the Pacific and appear to be closely related. No extinct species have this character.
Planktonic larvae	Allows more rapid dispersal, larger gene pool, release of larvae at smaller size, and production of more larvae per female.	Direction of evolution is unclear, but complete brooding may be a specialized condition.
Length of septum	A long septum implies a large foot relative to the size of the animal, and a relatively small brood area. It is associated with the need for firm attachment to the substrate.	The earliest known species of *Crepidula* have long septa. Direction of evolution cannot be inferred.
Shape of septum	The presence of notches and the position of attachment to the shell have no obvious functional significance.	One might assume that the septa which still show signs of coiling are more primitive, since all *Crepidula* spp. evolved from a coiled gastropod ancestor. But earliest preserved fossils already have straight septal margins.
Radial sculpture	Radial ribbing is common in sedentary gastropods. It confers strength to the shell. Spines may decrease settling of other filter-feeding biota, such as barnacles, on the shell.	Spines are easily derived from plicate radial sculpture. Ribbed species from the Western Atlantic are probably closely related (all have muscle scars as well). The earliest fossil calyptraeids are not ribbed.
Pigment	Loss of pigment occurs in photonegative species living on sites away from the light. This phenomenon is widespread among animals and plants. If metabolic energy is required to produce the pigment, those metabolic pathways may be lost when not needed. Color serves as camouflage (as in color polymorphic *C. convexa*) and absorbs heat.	Loss of color is a specialized trait, but is polyphyletic; it is suspected that it involves a very few genes.
Convexity	Genetic fixation of the trait for planar shape must give advantage fo photonegative species. Fixation is not complete in *Crepidula*; behavior (choice of substrate) is important.	Low convexity is the more specialized condition, as it correlates with a specialized habitat form of *Crepidula*.
Shell expansion rate	Rapid expansion rate represents flattening of the shell and rapid initial lateral growth. Functional significance is that rapid attainment of the adult limpet-like form and large foot may enhance survival in the environment where the spat settle.	Low expansion rate and high coiling are primitive characters; they are related to the ancestral spiral shell form.

sedentary older females. In all species, phenotypic plasticity obscures genetic variation.

It is imperative to understand which traits are interrelated and which vary independently. In a genome strongly modified by environmental factors, discrete, easily-scored traits such as banding patterns are rare. Also, shell characters are highly integrated. A *Crepidula* limited in substrate, such as *C. convexa* occupying a blade of eelgrass, is necessarily highly arched, has a deeply-

inserted septum, has a small aperture, tends to be thick-shelled, and produces fewer (not smaller) eggs. Another group of traits interrelated for purely mechanical reasons are: low convexity, low obliqueness, and a planar, shallowly-inserted septum, all occurring in individuals occupying concave surfaces. In taxonomic study, one must be aware that these are necessarily related characters, and attach significance to exceptions to these groupings.

Good taxonomic characters at the species level are those whose expressions are under direct genetic control, and which may vary independently from one another. Examples are the relative length of the septum, shape of the septal margin, position of muscle insertion, basic shape of the beak, sculpture pattern, color, and anatomical details such as the fringed mantle of *Crepidula onyx*. These traits are invariant under local environmental effects, including substrate differences, for 6 common species which I have examined in situ (*C. fornicata, C. onyx, C. plana, C. adunca, C. convexa,* and *C. norrisiarum*). They can be interpreted functionally (Table 3).

The radular teeth show intraspecific variation in cusp number, but are still valuable in species identification. The size of the individual teeth and the proportional relationships among the teeth differ in the 4 species for which I have studied radulae. The teeth of *C. plana* are smaller, relative to body size, than the teeth of the other species. But the marginals of *C. plana* are large compared with the centrals. The ratios of the length of the inner marginal to the width of the central tooth (averaged over 5 individuals of each species, and 3 rows per radula) are: *C. plana:* 6.0; *C. onyx:* 2.6; *C. convexa:* 2.6; *C. fornicata:* 3.2 (Nahant) to 3.6 (Martha's Vineyard).

2. Intraspecific variation over time

As a whole, *Crepidula* species have changed little since the Miocene. Many Miocene specimens are indistinguishable from modern representatives, as is true of many other mollusks. There have, however, been changes in degree of species variability. Some Miocene *C. fornicata* had longer septa, or were more coiled, or had a more rapid expansion rate than modern individuals. Since these traits are not likely to be strongly altered by the immediate environment, one can postulate high genetic variability within the species during that time span. Reduction in intraspecific variability and extinction of some species after a peak in the Miocene indicate some restriction of the group during the probably adverse conditions of intervening geologic time, when sea level changes affected shallow-water faunas.

If the Recent *Crepidula aculeata* and its larger Miocene relative are 1 species, it has been much reduced in size and thickness since the Miocene. The small representatives of *C. aculeata* have changed little, with intrapopulation variability in spine development evident from the initial appearance of the species. *C. princeps,* on the other hand, appears to have become less coiled (Addicott, 1970) and flatter (Grant & Gale, 1931) before it became extinct. Thus directional morphological changes through time are demonstrable in *Crepidula,* albeit rarely.

3. Affinities within the genus

Some authors divide *Crepidula* into several sections, subgenera, or even genera. Oldroyd (1927) places *C. nummaria, C. fimbriata,* and *C. nivea* in the subgenus *Ianacus* Mörch, and *C. lingulata* and *C. dilatata* in the subgenus *Crepipatella* Lesson. The subgenus *Crepidula* s. s., holds the remaining species. Gray (1867) uses the following generic names: *Crypta* for the species *aculeata, porcellana, fornicata, excavata, onyx,* and others, *Garnotia* for *adunca, Ergaea* for *walshi,* and *Noicia* for *chinensis.* Finlay (1927) erected the genus *Maoricrypta* for New Zealand species. Taki (1933, 1938) places nearly every species in its own genus or subgenus. His finer divisions include *Crepipatella, Siphopatella, Ianacus, Garnotia, Zeacrypta,* and *Neojanacus.* Thiele (1929: 248) uses 8 sections to discriminate groupings of *Crepidula.* The subgeneric designations used at various times for *Crepidula* are summarized in Table 4.

One may ask whether these divisions follow natural phylogenetic relationships, or whether they are based on convergence of shell form. *Maoricrypta* is based on geography and certainly has no taxonomic usefulness. The *Ianacus* group almost certainly is polyphyletic, as it is based on similarity in microhabitat and convexity, but includes differences in muscle insertion, shape of the septum, pigmentation, and larval type (note particularly *Crepidula monoxyla* and *C.*
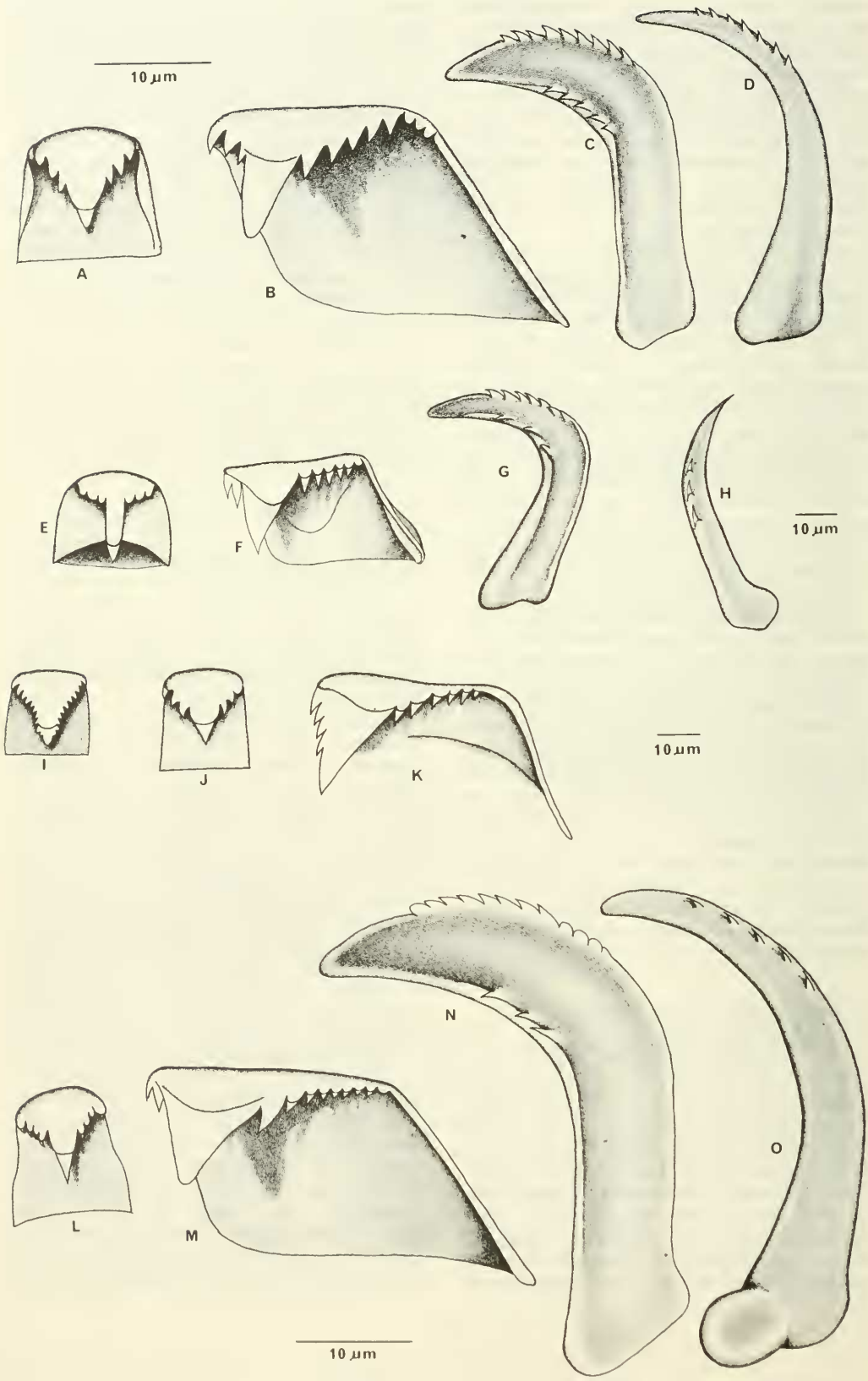
TABLE 4. Names which have been used to distinguish subgenera or sections in the genus *Crepidula*. Most have also been given generic standing, but they are synonyms of *Crepidula*.

Subgenus or "Section"	Author	Date	Type-species	Designated[1]	Senior synonym
Bostrycapulus	Olsson & Harbison	1953	*aculeata* (Gmelin)	O.D.	*Sandalium*
Crepidula, s.s.	Lamarck	1799	*fornicata* (Linnaeus)	M.	
Crepipatella	Lesson	1830	*dilatata* Lamarck	O.D.	
Crypta	Humphrey	1797	*fornicata* (Linnaeus) [synonym of *Crepidula*, s.s.] ; invalid	M.	
Dispotaea	Say	1826	*striata*[2]	M.	
Ergaea	H. & A. Adams	1854	*walshi* Reeve = *plana* H. Adams & Reeve	O.D.	*Siphopatella*
Galerus	Humphrey	1797	*chinensis* Linnaeus; [*Calyptraea*] invalid	O.D.	
Garnotia	Gray	1867	*adunca* Sowerby	O.D.	
Ianacus	Mörch	1852	*unguiformis* Lamarck	O.D.	
Maoricrypta	Finlay	1927	*costata* Sowerby	O.D.	
Noicia	Gray	1867	*chinensis* Gray	O.D.	
Sandalium	Schumacher	1817	*porcellana* (Linnaeus); sect. α *aculeata* (Gmelin); sect. β	O.D. O.D.	
Siphopatella	Lesson	1830	*walshi* Reeve	O.D.	
Zeacrypta	Finlay	1927	*monoxyla* Lesson	O.D.	

[1]M. = monotypy O. D. = original designation.
[2]*D. striata* is a *Calyptraea*. Thiele (1929) used *Dispotaea* as a section of *Crepidula*.

unguiformis). *Garnotia* consists only of *C. adunca* and its variants, certainly not worthy of subgeneric rank. *Crypta* is a synonym of *Crepidula*, which when used as a subgenus serves simply to catch all the forms which do not fit elsewhere. *Siphopatella* might be a useful subgenus, indicating forms with deep sulci and folds in the septum such as *C. walshi*. This character is conservative, not highly responsive to environmental pressures, and species which share it are closely related. Similarly, all species with produced septa (see Fig. 2) such as *C. adunca, C. norrisiarum*, and *C. costata* might be grouped together, with all forms possessing a single septal sulcus forming a 3rd group (suggested by McLean, personal communication). Although grouping the species by adhering to the septal character reveals possible phylogenetic affinities, the hierarchy created by subgeneric names is unnecessary and adds little to the understanding of the group. Such names should be based on more than a single shell character. Likewise, erection of the genus *Crepipatella* on the basis of the septum is unwarranted without anatomical confirmation. *Crepidula walshi* is as different from *Crepidula*, s.s., as is *C. dilatata*, but has typical *Crepidula* anatomy (Ishiki, 1936, 1939).

Table 5 is a grouping of the major fossil and Recent species of *Crepidula* on the basis of similarities in 5 characters. These characters were selected as the most important of those which can be seen from shell form and from field observations, in helping to define the ecological role of the species. They are: maximum size, convexity, pigmentation, microhabitat preferences, and the ability to form stacks of 3 or more individuals. Other traits, morphological as well as ecological, were then compiled for comparison. Some of the groups roughly parallel the subgenera just discussed. Suspected evolutionary affinities were disregarded in this analysis.

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FIG. 24. Radulae of 4 species of *Crepidula*. Compare the illustrations in Gray (1857) and Parodiz (1939). Formulae for the cusp arrangements are in the text. Shells from which these radulae were taken are in the Museum of Comparative Zoology, Harvard University.

C. convexa, based on 5 specimens from Woods Hole, Massachusetts, both sexes. A = central; B = lateral; C = inner marginal; D = outer marginal.

C. onyx, based on 7 specimens from Balboa, California, both sexes. E = central; F = lateral; G = inner marginal; H = outer marginal.

C. fornicata, based on 5 specimens from Nahant and 2 from Martha's Vineyard, Massachusetts, both sexes. I = central, Martha's Vineyard; J = central, Nahant; K = lateral, representative of both localities.

C. plana, based on 4 specimens from Woods Hole, Massachusetts, both sexes. L = central; M = lateral; N = inner marginal; O = outer marginal.

Fig. 25 presents another way of depicting the same type of relationship: a computer-derived cluster analysis of all species using all known morphological and ecological traits, unweighted. I used the unweighted-pair cluster technique, based on quantified simple matching coefficients (Sepkoski, 1974). There are a few differences, especially in groups 2 and 5, between the 2 treatments. The 1st treatment is more interesting in terms of ecological interpretation; the 2nd is presented only to show the degree to which the unweighted approach deviates from a logical weighted method.

Species known only as fossils are included in these analyses because I know about their morphology and paleoecology from the composition of the fossil assemblages, the substrate, and the specimens themselves (Arnold, 1903; Dall, 1892; Dubar & Taylor, 1962; Gardner, 1957; Woolman, 1898).

The following generalizations appear from Table 5:

Group 1: Large size is associated with convexity, planktonic development of numerous small eggs, the ability to form stacks and to live in muddy substrates, and (usu-

TABLE 5. Comparison of major morphological characters and ecological data. Division into 5 species groups is based on similarities in maximum size, habitat, ability to form stacks, pigmentation, and convexity. Groups 4 and 5 are divided on the basis of convexity and the presence or absence of a septal sulcus. See text for further explanation.

Species	Size (length)	Muscle scar	Stacks	Pigment	Convexity[1]	Preferred Substrate Exposed	Inside shells	Rostrate
Group 1								
costata	L	2	?	++	++	++	–	–
dilatata	L	1	++	++	++	++	–	–
excavata	L	1	?	++	++	++	–	++
fornicata	L	0	++	++	++	++	–	–
grandis	L	1	++	++	++	++	–	–
gregaria	L	?	++	?	++	++	–	–
lirata	L	1	?	?	++	++	–	++
onyx	L	0	++	++	++	++	–	–
princeps	L	1	++	++	++	++	–	–
"spinosa"								
(variant of aculeata)	L	1	?	++	++	++	–	–
Group 2								
adunca var. uncata	S	2	–	++	++	++	–	++
convexa	S	1	–	++	++	++	–	+
diminutiva	S	0	?	++	++	++	–	–
incurva	S	0	–	++	++	++	–	++
pileum	S	?	?	?	++	++	–	–
Group 3								
immersa	L	1	–	++	–	–	++	–
lessonii	M	0	–	+	–	–	+	–
monoxyla	M	2	–	–	+	++	++	–
nivea	L	0	–	–	–	–	++	–
nummaria	M	0	–	–	+	–	++	–
perforans	M	0	–	–	–	–	++	–
protea	M	0	–	–	+	+	++	–
striolata	M	0	–	+	+	–	+	–
unguiformis	M	0	–	–	–	–	++	–
walshi	M	0	–	–	–	+	++	–
Group 4								
aculeata	M	1	–	++	+	++	–	–
chinensis	M	?	–	–	+	++	+	–
dorsata	S	0	–	++	+	++	–	+
Group 5								
cymbaeformis	M	0	–	++	++	?	–	++
gibbosa	M	0	–	++	+	++	?	–
maculosa	M	1	–	++	++	++	–	–
marginalis	M	0	–	++	+	++	–	–
naticarum	M	1	–	++	++	++	–	++
norrisiarum	M	2	–	++	++	++	–	++
youngi	M	2	–	++	+	++	–	++

[1] High, > 1.35; low, 1.15-1.35; planar, < 1.15.

TABLE 5 (cont.)

Species	Septal area	Septal sulcus	Radial sculpture	Planktonic larvae	Inter-tidal	Preference for deep water (> 30 m)	Distribution in more than 1 zoogeographic province
Group 1							
costata	1/2	–	++	++	–	–	–
dilatata	1/3	++	–	?	–	+	++
excavata	1/3	–	–	?	–	?	–
fornicata	1/2	.+	–	++	–	+	++
grandis	1/2	–	–	?	–	?	–
gregaria	?	+	–	?	?	?	–
lirata	1/2	–	++	?	?	?	–
onyx	1/2	+	–	++	–	+	++
princeps	1/2	–	–	?	?	?	++
"spinosa" (variant of aculeata)	1/2	+	++	?	?	?	–
Group 2							
adunca var. uncata	1/4	–	–	–	++	–	++
convexa	1/3	–	–	–	++	–	++
diminutiva	1/2	–	–	?	?	?	–
incurva	1/2	–	+	–	++	–	–
pileum	1/3	–	–	?	?	?	–
Group 3							
immersa	1/4	–	–	?	–	–	–
lessonii	1/3	++	–	–	+	–	–
monoxyla	1/4	–	–	–	?	++	–
nivea	1/3	+	–	++	–	+	++
nummaria	1/3	+	–	–	–	?	++
perforans	1/3	+	–	–	++	–	++
protea	1/2	+	–	?	–	?	–
striolata	1/3-1/2	++	–	–	+	–	++
unguiformis	1/3	+	–	++	–	+	++
walshi	1/4	++	–	++	+	–	–
Group 4							
aculeata	1/3	++	++	–	++	+	++
chinensis	1/4	++	–	?	–	+	–
dorsata	1/4	++	–	++	–	++	++
Group 5							
cymbaeformis	1/2	–	–	?	?	?	–
gibbosa	1/3	+	–	?	+	?	–
maculosa	1/3	–	–	?	–	+	–
marginalis	1/2	–	–	?	+	?	–
naticarum	1/4	–	–	++	–	?	++
norrisiarum	1/3	–	–	–	–	++	++
youngi	1/2	–	+	?	–	++	–

KEY: L = large size; maximum length over 40 mm.
M = medium; maximum length between 25 and 40 mm.
S = small; maximum length less than 25 mm.
1/4, etc. = approximate proportion of apertural area covered by the septum.
0,1,2 = number of muscle scars.
++ = Strong, unambiguous expression of trait in question.
+ = Weak expression of trait.
– = Absence of trait.
? = Unknown.

ally) the absence of a septal sulcus. Traits which vary in their presence, or state of development, within this group are sculpture, muscle scar, and rate of whorl expansion. These happen to be traits which I have deemed important in judging evolutionary relationships. The species in group 1, including those known only as fossils, are (or were) capable of occurring in dense colonies and making their own substrate. They all have large septal areas for their size, perhaps due to the proportional relationship demanding that a large shell volume be supported by an even greater foot area.

Group 2: Small, convex species tend to brood their developmental stages through metamorphosis, live preferentially on shells or smooth stones or other living gastropods,

HOAGLAND
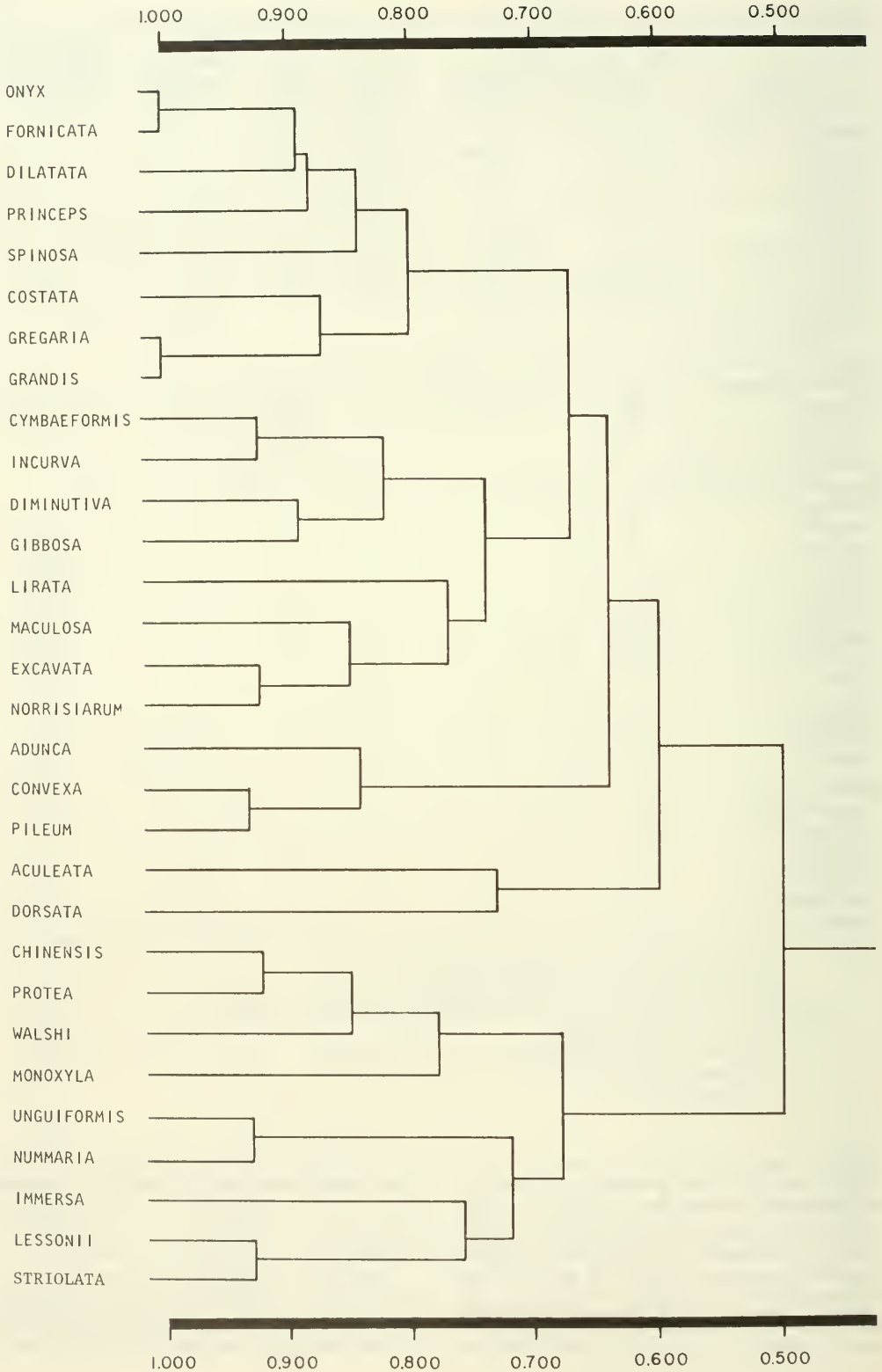
do not form stacks, lack a septal sulcus, and tend to be rostrate. They never dominate the community in which they live, in terms of biomass, as do members of group 1. Septal area in those known to brood the young to the crawling stage is small, perhaps allowing a proportionally larger brood area and smaller foot. Members of this group are hypothesized to be relatively poor long-distance colonizers unless transported as adults, but good at forming peripheral isolates necessary for speciation to occur.

Group 3: Members of this group, equivalent to the section "*lanacus,*" are of moderate size, planar to concave, do not form stacks, and are non-rostrate. The group can be subdivided into complete brooders and those with planktonic larvae, indicating either parallel evolution of 2 distinct planar *Crepidula* lineages, or polyphyletic origin of the 2 types of reproduction, or both. A polyphyletic loss of the planktonic larval stage in this and the above group is likely. The species in group 3, including the non-planktonic species, are good long-distance dispersers. Transport in the adult stage is facilitated by photonegativity and the tendency to live inside dead shells or on the underside of ships, or on other living organisms. Within group 3, short septal length is only weakly correlated with brooding habits ($r = 0.40$), perhaps because living in sheltered places this group is not so dependent on foot strength for protection from large predators as are other species. Also, the flat shell gives these species a lower ratio of area to volume than for convex species of *Crepidula.*

Group 4: These are small to mid-sized species, not rostrate, of low convexity, with prominent septal sulci. The preferred habitat is rocks or cobbles; stacking is rare or absent. *Crepidula dorsata* is broadly tolerant of physical conditions and is widely distributed latitudinally; *C. aculeata* is distributed world-wide at low latitudes. Thus no generalizations can be made on the zoogeography of the group.

Group 5: This group is not as homogeneous as the others, but simply contains highly convex species of intermediate size which usually prefer other living mollusks as substrates. They all have narrow ranges with indication of restricted temperature tolerances (*C. norrisiarum, C. naticarum,* and *C. maculosa* are limited to low latitudes). None of these species can be called successful by any of the traditional criteria, which are discussed later. This group is removed from group 4 on the basis of the shape of the septal sulcus, in addition to the 5 traits selected and described above.

From these analyses, the following conclusions are made:

1. In both fossil and Recent assemblages, one finds a mixture of species from these groups. In the Recent of Florida, we have *Crepidula plana, C. fornicata, C. convexa, C. aculeata,* and *C. maculosa* (1 from each group). In San Pedro Bay, California, there are *C. onyx, C. adunca, C. nummaria, C. nivea, C. norrisiarum, C. naticarum,* and rarely *C. aculeata* (2 from groups 3 and 5, and 1 from each of the others). *C. dorsata* lives outside the bay. Thus sympatric congeners are maximally spaced in morphological and ecological dimensions. In cold, rigorous environments, middle-sized forms (*C. aculeata, C. maculosa, C. norrisiarum*) drop out, broadening the distance between the remaining forms, decreasing substrate and food competition.

2. In general, evolution at the species level produces separation in substrate preferences, temperature tolerances, and life history parameters (indicated by differences in larval ecology) as well as morphological distinctions. Closely related, morphologically similar species do not co-occur. Sympatric species differ in life history strategies; for example, a fast-growing, early-maturing species suffering high pre-reproductive mortality (*Crepidula fornicata*) shares its substrate with a slower-growing, smaller species with different mortality schedules (*C. convexa*). The former has about 100 times as many offspring per brood as the latter.

3. Large maximum size correlates with planktonic larval development, while small maximum size correlates with lack of a planktonic stage. This has implications for the theory of r and K selection, because it had been assumed (Pianka, 1970) that large adult size correlates with brood protection,

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FIG. 25. Print-out of a computer cluster analysis (coefficient of association) which weights all morphological and ecological characters of *Crepidula* spp. equally. A quantified simple matching coefficient (Sepkoski, 1974) was used to cluster the data. The interpretation is given in the text. A few species were not included in the analysis, due to insufficient data.

fewer offspring and other "K" traits.

4. Length of the septum correlates with brooding habits and/or the need for strong attachment to the substrate. Species with pelagic stages tend to have proportionally larger septa and smaller brood areas. Planar species living in protected sites where foot strength is less important do not show this correlation. These hypotheses will be tested in a later paper.

5. Presence or absence of a strong muscle insertion (scar) has no clear relationship to substrate or habitat. It is indicative of genetic relationship. The same is true of whorl expansion rate and presence of a septal sulcus. These are considered to be conservative characters.

6. Stacking is found only in large species (and hence those with planktonic larvae). Population density is much greater in these species.

7. Speciation should be favored in groups without planktonic larvae in which gene flow is somewhat reduced and colonization is via adults. Colonization ability is high, however, even in lecithotrophic species.

8. Temperature tolerance seems to be important in imposing ultimate limits on the distribution of some species. Transport by man has shown that viable colonies can result from cohorts of less than 100 individuals. Females are able to store sperm, and hence 1 fertilized female could theoretically found a colony. *Crepidula* species are not functional hermaphrodites.

There is difficulty in constructing a phylogenetic tree of most genera, due to problems of: 1) convergence of characters; 2) uneven preservation, and complete lack of early fossils; 3) minor sequential changes being rarely preserved in the fossil record; and 4) inadequate information on the de-

TABLE 6. Species affinities. Species were grouped using the following "conservative" traits: shape and size of the septum, muscle scars, and beak characters. Types of larvae are indicated. Geographical affinities are listed as they exist within groups. Note the placement of white, planar *Crepidula* in more than one affinity group, according to this arrangement. The presence or absence of a planktonic larval stage is fairly consistant within groups, but there are exceptions. *C. aculeata, C. dorsata, C. incurva,* and several fossil species do not fit into any group. *C. excavata* shows some affinities with *C. maculosa* (shape of septum, muscle scar, and pigmentation). *C. convexa* and *C. maculosa* are similar in pigmentation in the southern part of the range of the former.

Species group	Shared taxonomic characters showing relationship	Geographical affinities	Variable characters
I. *C. fornicata* *C. gibbosa* *C. lessonii* *C. nivea* *C. nummaria* *C. onyx* *C. protea* *C. unguiformis (plana)*	No muscle scar; long septum with sinuous margin (or shallow sulcus); non-rostrate; beak turned to 1 side in a partial whorl; no radial sculpture; planktonic larvae (except *C. lessonii* and *C. nummaria*)	Worldwide except Asia and Africa	Size Convexity Pigmentation Preferred substrate Preferred depth Range of distribution
II. *C. dilatata* *C. excavata* *C. grandis* *C. gregaria?* *C. princeps*	Large, massive, inflated shell; 1 large, deep muscle scar; diagonal septum, attached far forward on the right side; no radial sculpture	Eastern Pacific	Septal sulcus Degree to which the beak is rostrate
III. *C. chinensis* *C. walshi*	Beak shows evidence of coiling; deep fold in septum, like a collapsed cup; not rostrate; no radial sculpture	Asian	Convexity Substrate preference
IV. *C. convexa* *C. maculosa*	One muscle scar; straight, short septum; beak slightly turned; very weakly rostrate	Western Atlantic	Size Pigmentation Depth and temperature preferences
V. *C. adunca* *C. costata* *C. monoxyla* *C. naticarum* *C. norrisiarum* *C. youngi*	Two muscle scars; sides of septum extend forward; short septum (except *C. costata*); beak uncoiled	Eastern Pacific; New Zealand; Australia	Size Pigmentation Convexity Substrate preference Rostrate beak Sculpture Larval mode

tailed anatomy of living forms. However, a breakdown of *Crepidula* species as to evolutionary affinities is possible (Table 6). Reasons for the arrangement of the species are summarized in the Table. The arrangement stresses the likelihood of a polyphyletic origin of white, planar species.

4. *Species distributions*

Distribution patterns over geologic time for the *Crepidula* species as summarized in this paper show several phenomena. For some (*C. dilatata, C. dorsata*), there is constant expansion, indicating constant spread without disjunction of the range or divergence of the species. Other ranges show little change over time, partly a function of relatively rapid initial spread and stabilization (*C. fornicata*), or of lack of spread altogether (*C. maculosa, C. costata,* and *C. norrisiarum*). Thirdly, there are species which show range contraction or shift as the world climate changed (*C. princeps, C. adunca,* and *C. aculeata*).

Thus *Crepidula* species have differentially responded to environmental change and to the time factor in evolution. This indicates differences in physiological capacities early in the history of the genus, which provided positive feedback to further create species divergence as they differentially expanded and contracted their ranges.

Saussaye (1869: 206) shows that *Crepidula unguiformis* extends through 4 marine provinces: the British, Celtic, Mediterranean, and Algerian. *C. nummaria* and *C. fornicata* are among the American species which extend through several provinces as well. These are generalists, which have a chance of long-term survival without drastic change as the environment changes.

An overall view of groups coexisting in North America and Europe from the early Tertiary to the Recent is found in Tables 7 and 8, and Figure 26. Dominant species are indicated. There is less clear-cut dominance

TABLE 7. Species found sympatrically in the major geologic formations, eastern continental United States.[1]

Age and formation or locality	Species	
Eocene		
Claiborne	*lirata*	* * *
L. Miocene		
Chipola	*fornicata*	*
	plana	(r)

TABLE 7 (cont.)

Age and formation or locality	Species	
M. Miocene		
Shoal River	*fornicata*	(r)
	plana	(r)
Calvert	*fornicata*	*
	spinosa (var.)	*
	plana	(r)
U. Miocene—L. Pliocene		
Choptank	*spinosa*	*
	fornicata	*
	plana	*
St. Mary's	*fornicata*	*
	spinosa	*
	plana	*
Yorktown	*spinosa*	* * *
	fornicata	* *
	cymbaeformis	*
	adunca	*
	aculeata	*
	convexa	*
	plana	(r)
Sankaty Head, Nantucket	*fornicata*	* *
	plana	* *
	convexa	(r)
	?spinosa	(r)
Duplin	*fornicata*	* * *
	spinosa	* * *
	cymbaeformis	* *
	adunca	*
	aculeata	*
	convexa	*
	plana	*
L. Pliocene		
Upper Choctawhatchee	*spinosa*	* * *
	cymbaeformis	* *
	fornicata	* *
	aculeata	*
	plana	*
M. Pliocene		
Florida	*maculosa*	* *
	fornicata	* *
	aculeata	*
	adunca	(r)
L. Pleistocene		
Waccamaw	*adunca*	* *
	aculeata	* *
	convexa	* *
	maculosa	*
	fornicata	*
	cymbaeformis	*
	plana	(r)
New Jersey	*fornicata*	*
Upper Caloosahatchee	*fornicata*	* *
	maculosa	* *
	aculeata	* *
	spinosa	*
	convexa	*
	cymbaeformis	(r)
	plana	(r)

[1]Formations are listed in order of descending age; species are listed in order of abundance: * * * very abundant; * * moderately abundant; * frequent; (r) rare. "Sympatry" is in the general sense, meaning found in the same deposit.

TABLE 8. Sympatric species in the western continental United States.[1]

Age and locality	Species	
Eocene		
Vader, Washington	*pileum*	(r)
Oligocene		
Washington	*praerupta*	*
	princeps	* * *
Miocene		
Oregon, Washington,	*princeps*	* * *
San Luis Obispo	(large oysters)	* * *
Pliocene		
Balboa Park, San Diego	*princeps*	* *
	onyx	* *
	nummaria	*
	norrisiarum	*
	adunca	* *
Soledad Mountains	*princeps*	
San Mateo	*princeps*	* * *
Los Angeles County	*princeps*	* * *
Ventura County	*princeps*	* *
Monterey	*nummaria*	*
Pleistocene		
Santa Barbara	*princeps*	*
Newport Bay	*onyx*	* *
	norrisiarum	*
	nummaria	(r)
Santa Monica	*naticarum*	*
Spanish Bight	*onyx*	* *
	adunca	*
Monterey	*perforans*	* *
Upper Pleistocene		
Palos Verdes and	*onyx*	* *
San Pedro	*norrisiarum*	*
	nummaria	* *
	adunca	*

[1]Formations are listed in order of descending age; species are listed in order of abundance: * * * very abundant; * * moderately abundant; * frequent; (r) rare.

in the Pacific faunas, and more species. This is probably due to the bulk of Pacific fossils being from the waters of California, where a rich fauna evolved compared with the Northern Atlantic. The result is the usual pattern of more species, with fewer individuals per species. Several species (*Crepidula dorsata, C. excavata*) are today obtained most often by dredging offshore, adding another dimension to the system not present in the Atlantic, where the same species living offshore also inhabit the tidepools.

During the Miocene, the largest species were dominant in numbers as well as biomass. Frequently, co-dominants existed at a single locality (e.g., *Crepidula fornicata* and *C. aculeata spinosa* at Yorktown, Virginia). In Recent faunas, species with narrow ranges (*C. maculosa,* for example) may be locally dominant, but another species may be more

frequent over the extent of the coastline. This distinction is lost in the fossil record where only a few isolated localities can be sampled and these generalized over the entire region.

Distribution data show that most species in the northern part of each coastline have broadly extending southern ranges, but the reverse is not true. There is only 1 exclusively boreal species, but several Panamic ones, adding to tropical species diversity.

5. *Evolutionary history of the genus*

One can see from data presented so far that *Crepidula* is a "successful" group, under 3 of the criteria which are used to measure this oft ill-defined quality: 1) continuance of basic types with little change since the early Miocene; 2) world-wide distribution of the genus, and of some species; and 3) abundance, in terms of biomass relative to other components of the assemblages, of the larger *Crepidula* species throughout their evolutionary history.

Crepidula specimens from the Cretaceous appear to have been scattered geographically, but this is an artifact of plate tectonics.

The genus was well-established and distributed by the Eocene, for specimens are found at scattered localities in California, Alabama, and possibly South America (von Ihering, 1907). Its greatest expansion in numbers of species and morphological variability came in the Miocene. This may be more apparent than real, because both coasts of America have well-preserved Miocene material. This might be explained by warmer temperatures and other conditions favorable to calcium carbonate deposition and preservation during this period.

The Pliocene was marked by the appearance of some new species, with most of the Miocene species surviving. Sea-level and temperature changes probably affected the generalist *Crepidula* species less than more specialized organisms, which suffered high extinction at this geologic boundary.

There were a few extinctions in the colder Pleistocene, notably *Crepidula princeps* and *C. cymbaeformis. C. adunca* disappeared from the Atlantic. There, it was a case of elimination of the intermediate-sized form, leaving 1 large (*C. fornicata*), 1 small (*C. convexa*), and 1 planar species (*C. plana*) in the North Atlantic. In the Eastern Pacific, however, it was the largest, previ-
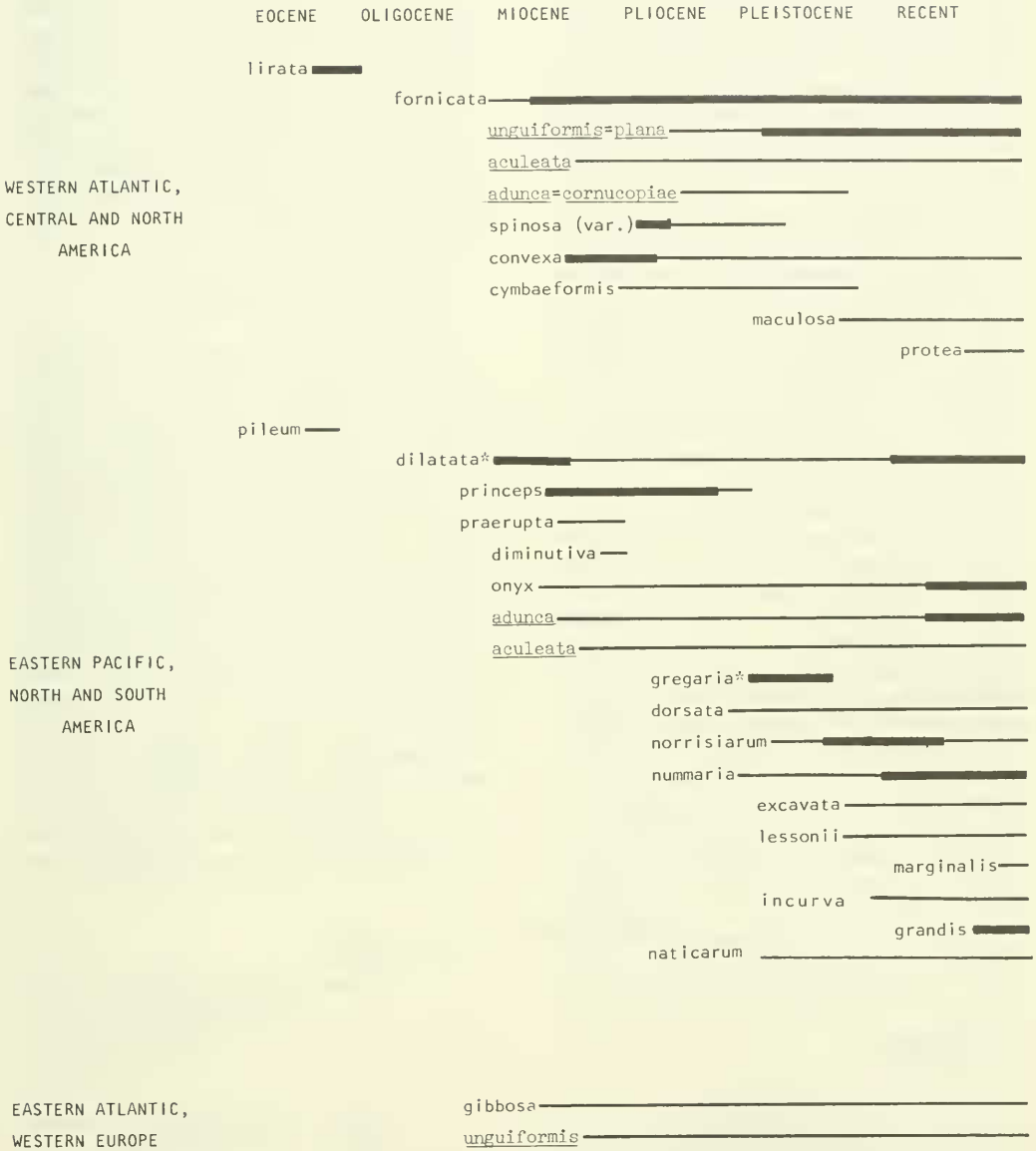
FIG. 26. Coexisting species of *Crepidula* in 3 geographical areas over time. Dominant species (in terms of numbers, relative to other calyptraeid species of the same time period) are indicated by heavy lines. Species found in more than 1 of the geographical areas are underlined. It is assumed that *C. plana* = *C. unguiformis* and that *C. cornucopiae* = *C. adunca*. Time periods are not to scale. An asterisk indicates a species which is restricted to South America. *C. praerupta,* probably a variant of *C. princeps,* is listed separately because it has a restricted temporal distribution. Several white species from the Pacific are not listed because they are not distinguishable from *C. nummaria* in the fossil record.

ously dominant species (*C. princeps*) which disappeared. The causes of its disappearance were probably not temperature and sea level fluctuations alone, but also biological factors related to its large size. Large filter-feeders require high concentrations of nutrients. Also, there is a limit to the size of organism which can be supported by the gill of a given size. In *C. princeps,* new demands of changing physical and biotic environments could have thrown the animals out of balance. California Pleistocene assemblages tend to have fewer large filter-feeding organisms than do earlier assemblages.

There have been no strong range contractions in the history of the genus. The center of evolution appears to have been the Panamanian region. From the earliest fossil records to the present, it appears that the Central American and Californian regions are the richest in *Crepidula,* with New Zealand-Australia also an endemic center; the Paris Basin and other European localities are relatively impoverished.

Convergence and parallel evolution have occurred in *Crepidula,* given similar selection pressures (microhabitats) in different parts of the world. Isolation of groups of species upon closure of the Panama gap allowed for the parallel evolution of 2 or more species of white, planar *Crepidula* (*C. lessonii* and *C. nummaria* versus *C. plana-C. unguiformis*). Convergence from *Calyptraea* or *Crucibulum* stocks is also a possibility to account for the peculiar folded septum in *C. walshi*; anatomical study will decide this point. Evidence for possible convergence to the planar *Crepidula* form is summarized in Table 6 and diagrammed in Figure 27. The pigmented *C. immersa* and the white *C. monoxyla,* both with muscle scars like other species endemic to Australia and New Zealand, are probably convergent with *C. unguiformis* rather than closely related to it. An example of the independent (convergent) evolution of single traits in different species groups could well be the tendency of some species to form stacks, which is limited ecologically to 1 member of any group of sympatric congeners. Lecithotrophy is another trait suspected of being polyphyletic.

6. *Evolution of the Calyptraeidae*

Possible paths of evolution within the family are shown in Fig. 28. The 1st calyptraeids appear in the lower Cretaceous (Shimer & Shrock, 1959). Schilder (1947) reported 13 genera of the Calyptraeacea by the Eocene, and 40 living currently, with bursts in the Upper Cretaceous and the middle to late Tertiary. The evolutionary sequence is that of flattening the shell, increasing the whorl expansion rate, and, in *Crepidula,* accentuating differential growth such that the shell becomes oblique (Fretter & Graham, 1962: 70-73). As shell coiling decreases, the columella becomes highly modified. In *Trochita,* it remains coiled; in *Calyptraea,* it is coiled or becomes prong-like (genus *Cheilea* Modeer, 1793); in *Crucibulum,* it becomes cup-like. In *Crepidula,* it is a simple partition; its function is the separation of the viscera, brood area, and
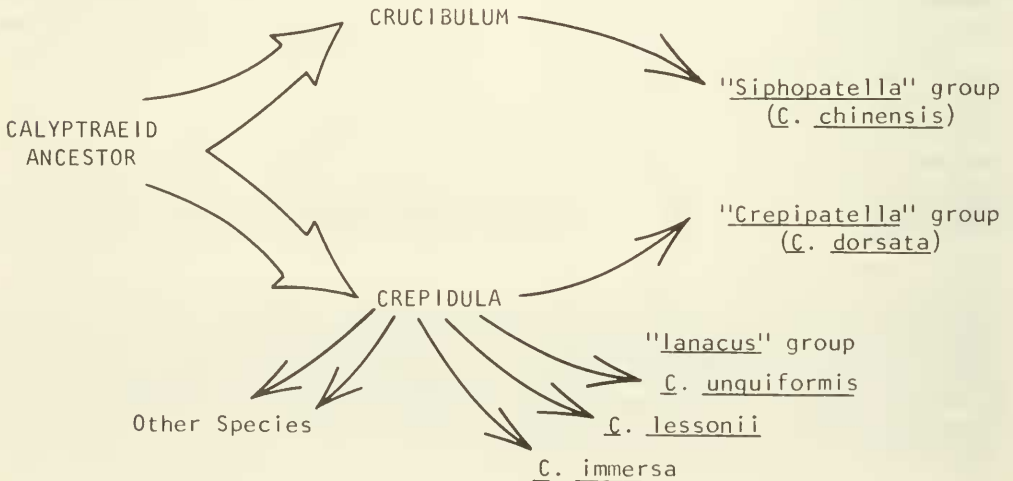
FIG. 27. Possible convergences in the evolution of *Crepidula* and *Crucibulum.*

TRICHOTROPID STOCK
Cold waters
Dredged

CALYPTRAEA
Tropical and subtropical

CRUCIBULUM
Low latitudes, primarily

EARLY CREPIDULA STOCK

CREPIDULA
World-wide

World-wide

CALYPTRAEID STOCK
Shell patelliform, but remnants of spiral still present

TROCHITA
Foot limpet-like
Shell aperture large
Good fossil record, Pacific Ocean

CAPULID STOCK
High patelliform shell
World-wide, especially tropical
Filter-feeders or facultative "parasites"

THYCA
Parasitic

ANCESTRAL MESOGASTROPOD
Shell coiled, operculate
Gill large, pectinibranch
Accessory sex organs
Sex determination labile
Capable of copulation

foot, which occupies a position analogous to that of a true limpet. The function of the columella in other gastropods, support of the visceral mass, remains.

Intermediate forms exist within *Calyptraea,* from species with several distinct whorls to *C. deformis,* which is quite limpet-like. Intermediates in septal form also mark the paths to *Crucibulum* and to *Crepidula* (both among extinct and living forms). Although the fossil record has not preserved the earliest *Crepidula,* it is likely that the branching point from the calyptraeid stock included forms much like *C. dorsata* in septal shape. The early species were probably small (less than 25 mm long), according to the records of *Calyptraea* from the Cretaceous. In the Eocene, we pick up large, robust species of *Crepidula* such as *C. lirata.* It is obvious that the highly modified *Crucibulum* could not have been the source for *Crepidula,* as suggested in 1 scheme by Taki (1933). I do agree with Taki that the *Ianacus* group is the most highly specialized and probably evolved last, but he did not recognize that it is most likely polyphyletic.

Within *Crucibulum,* the same kind of ecological segregation has taken place as in *Crepidula.* Although never achieving the prominence of *Crepidula* in population size and never becoming important in northern waters, the genus today is well-established in shallow offshore habitats, venturing into rocky tidepools. Like *Crepidula,* there are a few ribbed and a few spiny species, and 1 or 2 which become very large. There are lecithotrophic and planktotrophic species. Like all Calyptraeidae, they are protandrous (Coe, 1938). The group was well advanced by the Miocene, but in Tertiary assemblages *Crucibulum* is never as numerous as *Crepidula,* and rarely are more than 2 species found sympatrically.

FIG. 28. A possible scheme of major evolutionary events in the Calyptraeacea. **A.** Gill modified for feeding; protandry developed. **B.** Shell flattened for sedentary life; operculum lost. **C.** Increased whorl expansion rate. **D.** Modification for proboscis feeding. **E.** Filter-feeding further developed; septum modified into a curved plate. **F.** Shell and mantle growth further modified. **G.** Curved septal plate fused into a cup; secondary external radial symmetry. **H.** Columella unwound, but muscle still attached to it; growth asymmetric; septum flattened. **I.** Modifications in attachment of body to shell, such that the muscle(s) are affixed to the shell proper rather than to the septum.

Graham (1954) and Yonge (1962) discuss the genus *Trichotropis,* whose ancestor may be in common with the calyptraeids. *Trichotropis* has an operculum but lives a largely sedentary life on hard substrates, and has a proboscis but is also a filter-feeder. It is protandrous, and broods its young to the crawling stage under the foot. However, the shell is highly coiled and finely sculptured. *Trichotropis* is a boreal and deep-water genus; it is specialized and not an ancestral type. Its anatomical features suggest affinities with the family, but similarities with *Crepidula* in life history and niche are possibly convergent.

As for behavioral characters, an examination of fossil shells and a look at the biology of the more coiled living genera (*Trochita, Calyptraea*) reveal early development of the habits of sedentary existence, protandry, and filter-feeding (which capacity could have led to a selective regime favoring the sedentary existence, which in turn would favor protandry). The earliest fossil shells possess "mate marks," spots occupied by smaller members of the same species, from which copulation took place. The large Eocene species *Crepidula lirata* frequently shows a sudden decrease in shell convexity at about the size when sex change should have occurred (about 10-15 mm, based on comparison with a modern species of comparable adult size, *Crepidula fornicata*). This indicates, as demonstrated by Coe (1942b), Conklin (1898), and Boettger (1953), that the animal moved from a restricted substrate such as a female mate, to a less curved surface, such as a rock. This is known to occur at the time of sex change in many Recent species (e.g., *Crepidula convexa* and *C. fornicata* in areas where stacking does not occur).

Some species of *Crepidula* were fossilized in stacks, including Pliocene *C. princeps* from the Richfield Towers locality, Los Angeles, California. The specimens were preserved in a deposit from a turbidity current. *C. gregaria* from the Pleistocene of Patagonia is also preserved in stacks. In both cases, the *Crepidula* species are the dominant faunal elements, as are modern *C. fornicata* and *C. onyx* in areas where they form stacks (usually in muddy bays). One can assume similarity among these fossil and Recent species in life history characters such as birth rate, planktonic larval development, and sex change, given the similarity of ecological conditions, selection pressures, and the fact that they are related at the generic level. No other calyptraeid genera have been noted to form large stacks, but clusters of several small males on 1 female are common in Recent and fossil *Crucibulum* and *Calyptraea.*

It is of interest to ask how the package of traits came together as it did in *Crepidula* and in the family Calyptraeidae. I will treat this aspect of the evolution of the group, along with a study of intraspecific variability and niche size, in a subsequent paper on "adaptive peaks" and "species packing." But one may mention basic mesogastropod features such as a large pectinibranch gill (which allows for development of filter feeding), secondary sex organs and copulation (which allow for brood sac formation), and protandry, as important preadaptations in the early evolution of the calyptraeid mode.

Another question of interest is, which came first, planktonic or brood development of the young? All Calyptraeidae brood the young for some time; longer and longer retention is all that is required for conversion to full brood development. Similarly, shorter retention could lead from complete brooding to an intermediate stage with both brooding *and* planktonic development. Along with brooding comes a decrease in the number of eggs and an increase in egg size, factors which involve more complex evolutionary change. There is a veliger within the egg sac, but the velum is poorly developed.

7. *Ecological role of the calyptraeids*

The evolution of the calyptraeids filled an ecological role new for the gastropods. Calyptraeids are not convergent with patellids of other limpets except in having a protective cap-like shell, which is of general benefit to sedentary organisms and probably evolved in conjunction with filter feeding. Instead, they are ecologically convergent with oysters. It may be significant that the middle Cretaceous was a high point in numbers of oyster species. There was a decrease in oyster diversity at about the time the calyptraeids were evolving (the late Cretaceous). That conditions continued to be adequate for large filter-feeding shallow water mollusks is indicated by the huge size and population numbers (if not variety) of Eocene oysters, and by paleoecological temperature data, and the presence of rich,

shallow, marine deposits (Gardner, 1957). While calyptraeids certainly did not forcibly replace oysters (cause them to become extinct), they may have filled space left by groups as they became extinct. Or, they simply evolved in concert with the oysters in times good for sedentary filter feeders in general, surviving without much contraction, whereas many of the highly specialized oysters did not survive.

Similarities of calyptraeids with oysters include filter feeding (true archaeogastropod limpets are grazers), attachment to hard substrates, the ability to attach to each other to avoid mud and their own pseudofaeces, and the ability to change sex. Both groups possess extreme flexibility in shape. Grazing limpets cannot adapt themselves to any permanent site, for they must move to eat; instead, they often conform their resting spot to their shell by eroding the rock under them. Most oysters and all calyptraeids have some degree of brooding of young followed in some species by a planktonic stage. *Crepidula* can live at higher densities than can true limpets because they need not graze. Differences between calyptraeids and oysters include copulation in the former, and avoidance of regions with heavy siltation in the latter. Calyptraeids may also be compared with Anomiidae, a group of bivalves with an oyster-like life style.

A 2nd role taken up by the Calyptraeidae and new to mollusks is that of the white planar *Crepidula* species, which live inside dead shells or in other dark, protected places. This group has sacrificed access to strong water currents and is tolerant of silt; it is strongly photonegative. Those larvae which settle in protected places are under unique selection pressure, for conditions are quite different from those to which photopositive species are exposed. Loss of pigment is a common occurrence among animals occupying dark habitats. The plastic shape of *Crepidula* would have allowed some individuals to conform reasonably well to concave inner shell surfaces, before the planar tendency became genetically fixed.

Finally, some species of *Crepidula* have become adapted to the intertidal zone. Forms such as *C. convexa* attach themselves to intertidal as well as subtidal gastropods, and have little trouble surviving out of water for the time period of a tidal cycle. It is not difficult to see how this specialization came about, since many *Crepidula* species are only weakly selective in choice of substrate. Those which find themselves on *Littorina littorea,* for example, have a chance to survive only if they can withstand desiccation. The majority of *Crepidula* species are rarely found in truly intertidal situations, but do inhabit tidepools.

CONCLUSIONS

Crepidula is difficult taxonomically if only shell features are available. Constraints of their largely sedentary life style have caused convergences in shell form. Plasticity of size, shape, and even life history characters such as age at maturity, create enormous intraspecific variability. However, visibly expressed genetic differences are rare.

The natural environment of *Crepidula,* the shallow coastal regions, are unstable in geologic time. But in the fossil record, species survival is high, probably because most *Crepidula* species are physiological generalists, and all possess phenotypic plasticity.

The genus is successful world-wide in terms of species numbers, abundance, and persistence. Several large species with planktonic larvae (*Crepidula fornicata, C. onyx*) are nuisance organisms because of their success at colonization and multiplication. However, in the course of geologic time, some species which lack a planktonic stage have become as widely distributed. *Crepidula* species frequently transgress zoogeographic province boundaries, and interpopulation communication is high enough that centers of endemism are rare. Wright (1955) predicted that evolutionary change without splitting of the stock into localized species should prevail when local demes have high gene flow (and, I would add, similar selective regimes). This appears to be the case in *C. adunca, C. aculeata,* and other *Crepidula.*

Modes and rates of speciation and evolutionary change are difficult to quantify. I hypothesize that there should be differences between the species with pelagic and nonpelagic development because the pelagic developers produce about 100 times as many offspring, with intense selection pressure on the young. Also, they tend to have much more densely packed adult populations, have gregarious spat, and have more widespread and complex distribution of offspring.

The fossil record of the family Calyp-

traeidae does not clearly reveal the order of evolutionary events, except to suggest that the group evolved rapidly once a few critical steps were attained. These were adaptation of the gill for filter feeding, which allowed sedentary life (made more efficient by copulation and protandry), which in turn allowed the brooding of young under the foot.

Work remaining to be done on *Crepidula* includes taxonomic study of African species, and anatomical examination of all species, especially the white, planar forms. More complete data on reproduction and life history of all species are needed to test the hypotheses I have constructed. Because of their wide latitudinal distribution and differences in reproduction and behavior, *Crepidula* species can become important organisms in the study of population genetics, ecology and evolution, now that the general systematics are better understood and updated.

ACKNOWLEDGMENTS

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INDEX TO SCIENTIFIC NAMES